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Studies in plant physiology.

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No. 19

Studies in Plant Physiology

Factors in Elongation and Expansion under Reduced Light Intensity —Frederic E. Clements and Frances L. Long

Further Studies of Elongation and Expansion in *Helianthus* Phytometers—Frederic E. Clements and Frances L. Long

Effect of Soil Temperature on Transpiration in *Helianthus Annuus* —Frederic E. Clements and Emmett V. Martin

Studies of the Effect of Artificial Wind on Growth and Transpiration in *Helianthus Annuus* —Emmett V. Martin and Frederic E. Clements

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Application of Calorimetric Methods to Ecological Research —Frances L. Long

A Large-Capacity Drying Oven With Constant Uniform Temperature and Forced Ventilation—Emmett V. Martin

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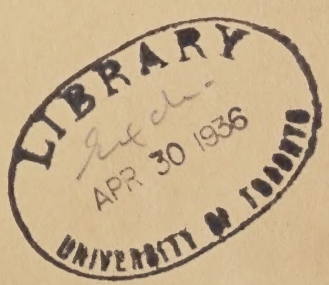

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Washington, D. C.
January 15, 1936

Reprinted from Plant Physiology, 9: 767–781, 1934.

FACTORS IN ELONGATION AND EXPANSION UNDER REDUCED LIGHT INTENSITY

Frederic E. Clements and Frances L. Long

In seeking to determine the rôle of factor and function in adaptation in nature, the first step has been to deal under control with one factor, and the function directly concerned, by equalizing the others. As an outcome of the results thus secured, it has been possible to modify the method to take into account two variables, such as light and water, in the hope of evaluating their respective rôles. This is particularly desirable in the case of adaptation to shade, in which reduced light intensity has generally been regarded as the controlling agent, with little or no consideration of water relations. Since water serves both as a raw material and as a mechanical force in growth, it would seem on theoretical grounds to play a significant part in such modification. This assumption has been borne out by the behavior of ecads in nature and especially by that of transplants in shade at times and seasons when the water content was deficient. The present account deals with the investigation of the mutual relation of light and water as exhibited by growth and modification in a series of lath-houses, which have been found to afford better control than cloth tents.

Experimental technique

The standard phytometer method was employed, in which are utilized galvanized iron containers 8.5 inches wide and 11 high, provided with removable lids containing a 2-inch hole to accommodate the stem and a watering tube. A layer of coarse gravel an inch thick was placed in the bottom of the can and the weight of the latter then adjusted to a total of 2000 gm. by varying the gravel. Air-dry loam to the amount of 6600 gm. was added, together with 1320 gm. of water or 20 per cent. of the dry weight, and the containers left over night to permit even penetration. In filling each can, the glass tube 1.5 cm. across was held against the bottom to prevent clogging and was raised a half centimeter at the first watering to allow ready absorption.

After soaking the sunflower seeds over night, five were placed near the center of the container and allowed to germinate in the greenhouse. By two weeks after planting, the first pair of true leaves were well developed, and all but one of the seedlings in each can were pulled out. In this operation much care was taken to select individuals for uniformity in height and the size of the leaves.

The essential feature of the experimental procedure was to vary the holard under each of several degrees of light intensity, though the installation was improved in certain details through the five series. The first two sets were preliminary in nature and only the two extremes of holard, namely, 35 and 13 per cent., were used. In the remaining series, there were four different water contents and either three or four effective intensities of light. The technique is best illustrated by series V in which 96 phytometers were utilized. These were organized into four batteries of 24 each, to three of which water was added by weight to bring the holard to 35, 26, and 18 per cent. of the dry weight. Since the soil used is saturated at 42 per cent., the values represented respectively 83, 62, and 43 per cent. of saturation. No water was added to the fourth battery, which was allowed to dry out until the water content reached 13 per cent. or 31 per cent. of saturation. A layer of 500 gm. of sand was employed to prevent evaporation but at the same time to permit adequate aeration. Finally, the lid was put on the can, the glass-tube stoppered, and a seal of non-absorbent cotton wrapped about the stem in such manner as to completely close the opening.

In this series the light gradient comprised four intensities, *viz.*, full sunlight, 32, 16, and 8 per cent. of sunlight as afforded by the group of lath-houses. A battery of 24 phytometers was installed in each of the latter, as well as in the sun, where the containers were placed in a wooden box sunken in the soil to prevent overheating of the walls and consequent interference with root functions. As indicated previously, each battery embraced four different holards, represented by six phytometers each. The higher value of 35 per cent. was the maximum for the soil, since an occasional effect of deficient aeration was found in the lower light intensities, while the extreme of 13 per cent. now and then permitted slight wilting under high insolation. A strain of *Helianthus annuus* with simple stems was used in all series, and this was supplemented in the last one by *Clarkia elegans,* a California annual with exceptional adaptability to shade.

Though it was impossible to equalize temperature and humidity in the garden and the lath-houses, the difference in average daily maximum temperature was but 1.5° F. and between average daily minima 4° F. throughout the spring period. There were only 3 degrees' difference in average temperature, this being highest in the lath-house of 16 per cent. intensity and the same in the sun and the lath-house with 8 per cent. The average humidity varied somewhat more, being nearly uniform in the lath-houses but rising several degrees in the sunlight, probably owing to the sea breeze. While the alternation of factor changes is more regular in lath-house than in forest, it is evident that it is of the same nature as that between sun-fleck and shadow below such a canopy.

The water content was kept practically constant by weighing the con-

tainers from time to time and replacing the amount of water lost. Frequent weighings were not necessary during the first few weeks while the plants were small, but as they grew larger, replacement was required more often. During the last week when temperatures were high, some individuals lost more than a liter of water per day in the sun and thus demanded weighing and watering at two-hour intervals to maintain the proper holard. In addition to the water requirement, the rate of growth in stem and leaf was traced week by week, and the wet and dry weights of each plant were ascertained at the close of each series. Measurements of stem height and diameter and of the length and width of each leaf were made each week at the same hour and in the same sequence. Leaf areas were calculated by the formula $L \times W \times 1.3$, which gives the combined area of the two sides (CLEMENTS and GOLDSMITH, "The Phytometer Method," 1924: 35); this method was again verified for the strain of sunflowers employed.

Results from series V

This was not only the most complete of the various series, but it also coincided with the time of the year when the adaptation sequences were at their optimum in the Santa Barbara climate, namely, during April and May. Series IV occupied the period of January to April, and number III that from October to December. The criteria employed were height and diameter of stem, number and area of leaves, wet and dry weights of the whole plant, water requirement and transpiration. For the sake of ready comparison, the data are presented in two sequences, *viz.*, arranged under the four holards in accordance with light intensities, and in the four light values by the percentage of holard.

With respect to the growth of the stem, the results were essentially consistent for diameter, the maximum occurring in 35 per cent. holard and sunlight and falling off rather regularly with reduced light. A slight discrepancy is found in sunshine for 18 per cent. and 13 per cent., owing to the fact that the rate of supply occasionally lagged behind water loss. The response in height was less consistent only to the extent that the maximum alternated between 16 per cent. and 32 per cent. light. On the other hand, the integration of stem growth as represented by height diameter (H/D) yielded a regular rise with decreasing light, only the extreme condition of 13 per cent. holard and 8 per cent. light being out of accord. Leaf area diminished with all but perfect regularity in harmony with light values, dropping very rapidly in the two lowest intensities, while there was no exception to the regular decrease in the number of leaves.

As was anticipated, functions in general and the relatively simple transpiration in particular exhibited the closest correspondence with factor gradients. Water loss was uniformly highest in the sun and fell off sharply

in light of 32 per cent. However, the greatest decrease was between 32 per cent. and 16 per cent., where it was threefold, or even sevenfold in 13 per cent. holard. The loss per cm.^{2} agreed with the total except for the lower three water contents in the 8 per cent. lath-house, a discrepancy probably associated with the small leaf area, crowded stomata, and thinner cuticle. In agreement with transpiration, both wet and dry weights dropped with light intensity, but the dry weight diminished more rapidly, the maximum being respectively 23, 23, 12, and 15 times the minimum in each holard, by contrast with 13, 12, 6, and 8 for the wet. On the other hand, the water

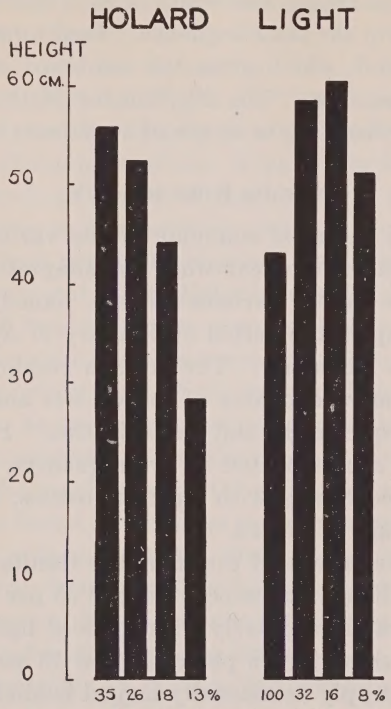

FIG. 1. Average stem heights for holard and light in the three series.

requirement rose steadily with weaker light, with the exception of the 13 per cent. holard, and this is to be explained by the fact that food-making decreased faster than water loss as the energy fell off, as shown by ratios of 23, 23, and 12 in the former, and 15, 11, and 7 in the latter.

Turning to gradients of holard under each of the four light intensities, stems were shorter in response to lower water values, with two exceptions, while diameters lessened in every case. Leaf areas followed the rule with but two insignificant discrepancies, and the number of leaves decreased throughout. Total transpiration is similarly in accord with the holard, as

is likewise the wet weight. Dry weight is slightly less harmonious, lack of aeration becoming perceptible in 35 per cent. holard, while the water requirement is all but entirely consistent.

Results from series III and IV

In addition to *Helianthus,* series IV contained *Clarkia elegans,* a native annual especially tolerant of shade. The holard gradient was the same, but the reduced light intensities were but two, namely, 16 per cent. and 8 per cent. As a consequence, the tallest stems were always found in the 16 per cent. value, while as before the stature was distinctly greater in 8 per cent. than in sunshine. The diameter of stem diminished consistently with the

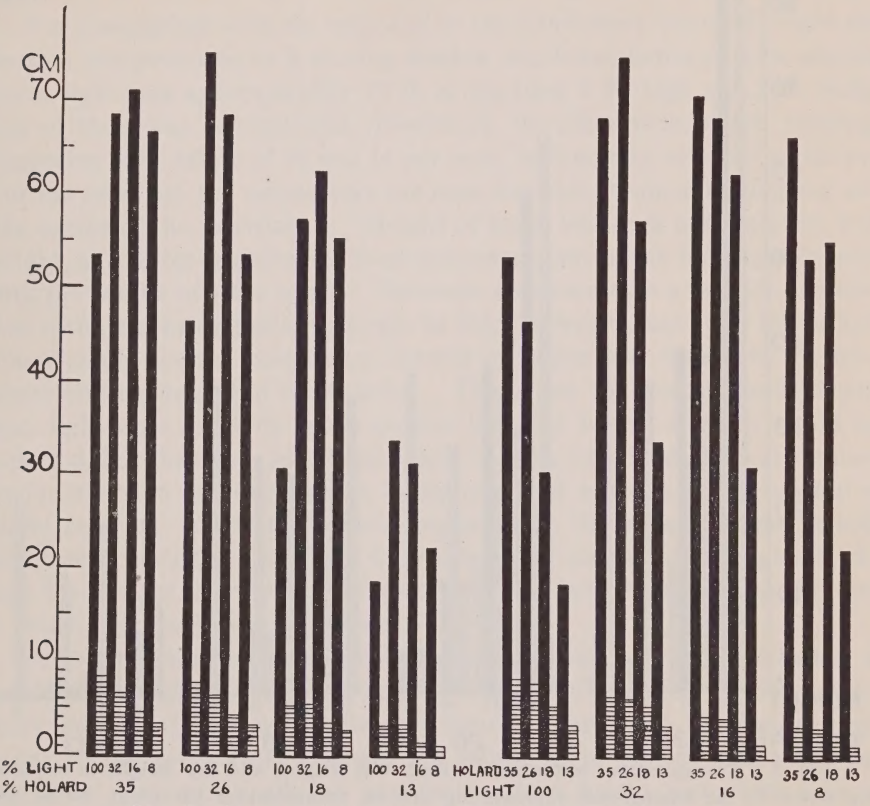

FIG. 2. Stem height (×1) and diameter (×5) in series V.

three intensities, as did also leaf area, number of leaves, wet and dry weights; conversely, height/diameter of stem was enhanced. Total transpiration fell off in entire harmony with light reduction, as did likewise the water loss per cm.,^{2} with the exception of a slight rise in 8 per cent. under

13 per cent. holard. By contrast, the water requirement rose regularly except for a small discrepancy in 8 per cent. light and 26 per cent. water content. The values for the holards within each light intensity were less consistent, the plants in 26 per cent. usually growing better than those in 35 per cent. This discrepancy seems to be explained by the fact that this

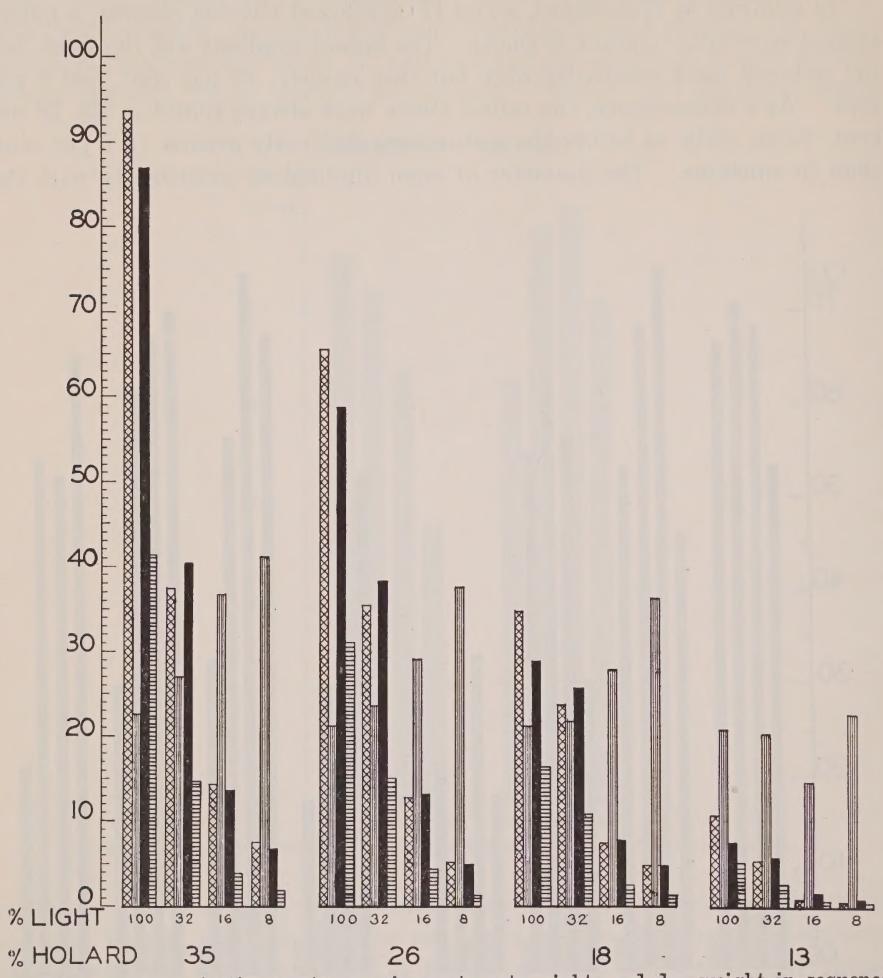

FIG. 3. Transpiration, water requirement, wet weight, and dry weight in sequence for series V, the basing unit representing 100 cc. transpiration per plant, 10 cc./gm. water requirement, 4 gm. wet wt. and 1 gm. dry wt.

series was begun in January when transpiration did not compensate for the high water content and the resulting tendency toward deficient aeration.

The relations of stem and leaf to the factor gradients were distinctly less uniform for *Clarkia*. Wet and dry weights dropped consistently with

both light and holard, as did likewise the total transpiration, but maximum stature and leaf size alternated between sun and 16 per cent. light. Stem diameter was more regular in response, but water requirement was quite erratic. The divergence in behavior as compared with the sunflower is probably to be ascribed to the necessity of transplanting the individuals as seedlings, thus favoring the production of lateral shoots to the disadvantage of the main stem.

Series III represented the original installation that was duplicated in IV, and was grown from October to December of the preceding autumn. The two corresponded almost exactly in the trend of results, except that water requirement in the earlier set was uniformly higher in 16 per cent. light.

For comparison with the response in the lath-houses where the light reduction was produced by a moving shadow, sunflower batteries were placed under light arcs approximately 10 ft. at the base, 6 ft. high and 3 ft. wide. One of these was covered with cheesecloth, the other with paper, yielding respective light values of 62 and 14 per cent., by contrast with full sunshine. For the gradient, the values were the most variable obtained during the entire course of the experiment. Height of stem, leaf area and number, wet weight, and water requirement were not concordant in the four holards, nor with the results in other series. However, diameter gave a positive correlation with decreasing radiant energy, as did dry weight and total transpiration, a single marked exception occurring in 13 per cent. holard in the sun, where wilting disturbed the relation. The values for sunlight and 62 per cent. light were regularly much greater than for 14 per cent., as would be expected, but they were also much closer to each other and alternated more frequently than the difference in intensity would warrant on the basis of a direct relation. Aside from water requirement, the values for the holard sequence in each light intensity were essentially consistent throughout, except for a slight decrease in the 35 per cent. in both degrees of shade, due it would seem, to deficient aeration.

In order to test the rôle of water in combination with another factor, a third subseries of the same four holards was grown under three wind conditions, namely, 0, 5, and 10 miles per hour. Apart from the 5-mile wind under 13 per cent. water content, the results as to growth and water requirement were practically all consistent. Stem height and width gave a negative correlation with increasing velocity, the two being in harmony with each other instead of opposed, as in the case of light. The leaf area and number also fell off as the wind velocity rose, as did wet and dry weight, while the water requirement was augmented. The total transpiration was highly variable, but the water loss per cm.^{2} rose with much regu-

TABLE I

RESULTS FROM SERIES V

FACTOR GRADIENTS		STEM					LEAF AREA PER PLANT		LEAVES	
HOLARD	LIGHT	HEIGHT		DIAM.		H/D				
%	%	*cm.*	%	*cm.*	%		*sq. cm.*	%	*No.*	%
35	100	53.3	100	1.66	100	32.1	4556.6	100.0	23.7	100
	32	68.3	128	1.30	78	52.5	3124.5	69.0	18.5	78
	16	70.9	133	0.91	55	72.8	1122.3	25.0	14.3	60
	8	66.3	125	0.68	41	97.5	648.6	14.0	12.5	53
	Ave.	64.7	122	1.14	69	63.7	2458.5	52.0	17.2	73
26	100	46.3	87	1.58	95	23.9	3420.0	75.0	22.2	94
	32	75.0	141	1.25	75	60.0	2641.5	58.0	18.0	76
	16	68.3	128	0.83	50	82.3	1195.5	26.0	13.2	56
	8	53.5	100	0.61	37	87.8	435.8	10.0	11.3	48
	Ave.	60.8	114	1.07	64	63.5	1923.2	42.0	16.2	69
18	100	30.5	57	1.05	63	29.1	1743.3	38.0	17.2	73
	32	57.3	108	1.08	65	53.0	1939.1	43.0	15.2	64
	16	62.5	117	0.71	43	88.0	727.2	16.0	12.3	52
	8	55.3	104	0.55	33	100.5	439.6	10.0	11.0	46
	Ave.	51.4	97	0.85	51	67.9	1212.3	27.0	13.9	59
13	100	18.8	35	0.65	39	28.9	521.5	11.4	12.2	51
	32	33.6	63	0.66	40	51.0	499.6	10.9	10.5	44
	16	31.0	58	0.28	17	111.0	114.2	2.5	8.2	35
	8	22.1	41	0.23	14	96.0	65.2	1.4	6.1	26
	Ave.	26.4	49	0.46	28	71.7	300.1	6.6	9.3	39

FACTOR GRADIENTS		TRANSPIRATION		WEIGHT OF PLANT			WATER REQUIREMENT	
HOLARD	LIGHT	TOTAL	GM./ SQ. CM. MAY 7–14	WET	DRY	RELATIVE WEIGHT		
%	%	*cc.*	*gm.*	*gm.*	*gm.*	%	*cc./gm.*	%
35	100	9359.0	134.5	347.7	41.23	100.0	227	100.0
	32	3727.0	80.9	162.1	13.70	33.0	272	120.0
	16	1428.0	78.5	54.2	3.88	9.4	368	162.0
	8	741.5	64.2	26.6	1.80	4.4	412	181.0
	Ave.	3563.9	89.5	147.7	15.15	36.7	320	141.0
26	100	6564.3	99.6	234.9	31.02	75.0	211	92.9
	32	3535.5	78.4	153.2	15.00	36.0	236	104.0
	16	1290.0	64.5	52.4	4.43	11.0	291	128.0
	8	508.1	68.5	19.1	1.35	3.3	376	165.6
	Ave.	2974.5	77.8	114.9	12.95	31.3	279	122.6
18	100	3647.0	103.0	115.7	16.35	40.0	212	93.4
	32	2383.6	70.5	102.7	10.95	27.0	218	96.0
	16	748.5	59.0	31.8	2.68	6.5	279	122.9
	8	485.1	61.1	19.5	1.33	3.2	365	160.8
	Ave.	1771.1	80.9	67.4	7.83	19.2	269	118.3
13	100	1057.0	114.7	30.0	5.08	12.3	208	91.6
	32	527.5	69.1	22.8	2.63	6.4	201	88.5
	16	83.8	52.2	5.9	0.58	1.4	145	63.9
	8	79.1	79.7	3.7	0.35	0.9	226	99.0
	Ave.	434.9	78.9	15.6	2.16	5.2	195	85.7

TABLE I—(*Continued*)

RESULTS FROM SERIES V

FACTOR GRADIENTS		STEM					LEAF AREA PER PLANT		LEAVES	
LIGHT	HOLARD	HEIGHT		DIAM.		H/D				
%	%	*cm.*	%	*cm.*	%		*sq. cm.*	%	*No.*	%
100	35	53.3	100	1.66	100	32.1	4556.6	100.0	23.7	100
	26	46.3	87	1.58	95	29.3	3420.0	75.0	22.2	94
	18	30.5	57	1.05	63	29.1	1743.3	38.0	17.2	73
	13	18.8	35	0.65	39	28.9	521.5	11.4	12.2	51
	Ave.	37.2	70	1.24	74	29.9	2560.3	56.1	18.8	80
32	35	68.3	128	1.30	78	52.5	3124.5	69.0	18.5	78
	26	75.0	141	1.25	75	60.0	2641.5	58.0	18.0	76
	18	57.3	108	1.08	65	53.0	1939.1	43.0	15.2	64
	13	33.6	63	0.66	40	51.0	499.6	10.9	10.5	44
	Ave.	58.5	110	1.08	65	54.1	2051.2	45.2	15.6	66
16	35	70.9	133	0.91	55	72.8	1122.3	25.0	14.3	60
	26	68.3	128	0.83	50	82.3	1195.5	26.0	13.2	56
	18	62.5	117	0.71	43	88.0	727.2	16.0	12.3	52
	13	31.0	58	0.28	17	111.0	114.2	2.5	8.2	35
	Ave.	58.2	109	0.68	41	88.5	789.8	17.4	12.0	51
8	35	66.3	125	0.68	41	97.5	648.6	14.0	12.5	53
	26	53.5	100	0.61	37	87.8	435.8	10.0	11.3	48
	18	55.3	104	0.55	33	100.5	439.6	10.0	11.0	46
	13	22.1	41	0.23	14	96.0	65.2	1.4	6.1	26
	Ave.	49.3	93	0.52	31	95.5	397.6	8.9	10.2	43

FACTOR GRADIENTS		TRANSPIRATION		WEIGHT OF PLANT			WATER REQUIREMENT	
LIGHT	HOLARD	TOTAL	GM./SQ. CM. MAY 7–14	WET	DRY	RELATIVE WEIGHT		
%	%	*cc.*	*gm.*	*gm.*	*gm.*	%	*cc./gm.*	%
100	35	9359.0	134.5	347.7	41.23	100.0	227	100.0
	26	6564.3	99.6	234.9	31.02	75.0	211	92.9
	18	3467.0	103.0	115.7	16.35	40.0	212	93.4
	13	1057.0	114.7	30.0	5.08	12.3	208	91.6
	Ave.	5111.8	113.0	182.1	23.42	56.8	215	94.5
32	35	3727.0	80.9	162.1	13.70	33.0	272	120.0
	26	3535.5	78.4	153.2	15.00	36.0	236	104.0
	18	2383.6	70.5	102.7	10.95	27.0	218	96.0
	13	527.5	69.1	22.8	2.63	64.0	208	88.5
	Ave.	2544.4	74.7	110.2	10.57	40.0	234	102.1
16	35	1428.0	78.5	54.2	3.88	9.4	368	162.0
	26	1290.0	64.5	52.4	4.43	11.0	291	128.0
	18	748.5	59.0	31.8	2.68	6.5	279	122.9
	13	83.8	52.2	5.9	0.58	1.4	145	63.9
	Ave.	887.6	63.6	46.0	2.89	7.1	271	119.2
8	35	741.5	64.2	26.6	1.80	4.4	412	181.0
	26	508.1	68.5	19.1	1.35	3.3	376	165.6
	18	485.1	61.1	19.5	1.35	3.2	365	160.8
	13	79.1	79.7	3.7	0.35	0.9	226	99.0
	Ave.	453.5	68.4	17.2	1.21	2.9	345	151.5

larity in the higher water contents, the relative values being 2, 3, 5 for 35 per cent. and 1, 2, 3 for 18 per cent.

With respect to the holard gradient under the several velocities, stem height and diameter diminished with reduced water values, and this was equally true of leaf area and number, as likewise of wet and dry weights. The same rule held for water requirement with a single exception, and applied consistently to the total water loss but less regularly to transpiration per unit of leaf area.

TABLE II

COMPARISON OF RESULTS FROM THE THREE SERIES

	HOLARD-LIGHT			LIGHT-HOLARD		
	V	IV	III	V	IV	III
Stem						
height	m16–32	m16	m16	−r	m26	−r
diam.	−r	−c	−r	−c	−r	−r
ht./diam.	+r	+c	+r	d	−d	−r
Leaf						
area	−r	−c	−c	−r	m26	−c
number	−c	−c	−c	−c	m26	−r
Weight						
wet	−c	−c	−c	−c	m26	−c
dry	−c	−c	−c	−r	m26	−r
Transpiration						
total	−c	−c	−c	−c	m26	−r
per cm.^{2}	−r	−r	−d	−d	−r	−d
Water require.	+r	+r	m16	−r	d	d

In the above table, positive correlation with the decreasing gradient of light or holard is shown by the minus, negative by the plus sign: *c,* denotes consistent, *r,* regular, and *d,* discrepant. Where the maximum is out of the sequence, it is indicated by *m* with a figure for the condition. The agreement between the three series is close in the case of light, especially in view of the fact that the sun's altitude was respectively that of spring, winter, and fall. The accord is distinctly less for holard, by reason of the divergence of the fourth series for the most part, but also, it would seem, because of the unavoidable variation of holard in the interval between two waterings.

When the results in stem height are averaged for the three series, they yield the following percentages in the order of descending holard, *viz.,* 100, 93, 77, and 50, while for decreasing light the values are 100, 136, 140, and 118. For stem diameter, the respective figures in the same sequence are

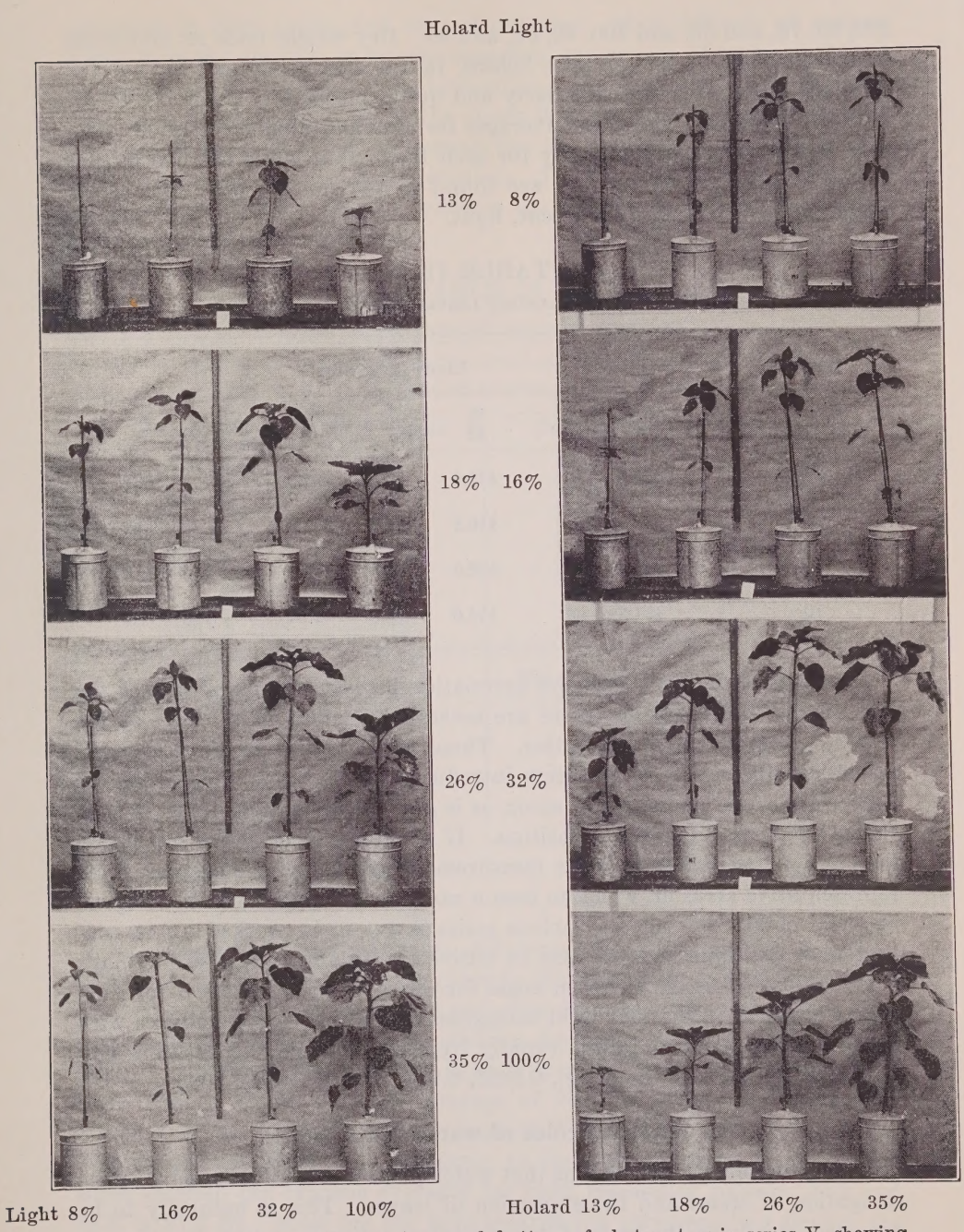

FIG. 4. A representative set from each battery of phytometers in series V, showing the growth under the various conditions.

100, 99, 78, and 58, and 100, 82, 61, and 49. Dry weight finds its maximum of 121 per cent. in 26 per cent. holard, falling then to 65 and 28, but for the light gradient it falls regularly and quite consistently from 100 to 45, 16 and 7 per cent. The grand averages for area and number of leaves drop with almost complete regularity for each factor, but while the five largest leaves for 35 per cent. holard are found in the sun, for all other water contents they occur in 32 per cent. light.

TABLE III

EXPANSION OF LARGEST LEAVES, SHOWN IN CM.^{2}

HOLARD	LIGHT INTENSITY			
%	% 100	% 32	% 16	% 8
35	553.8	475.0	204.0	141.2
26	378.8	416.2	205.8	98.2
18	303.4	352.0	144.0	101.2
13	127.2	144.6	29.4	17.3

There is evidently a negative correlation between the expansion of the leaf and its thickness, but there are several difficulties in the way of the ready determination of the latter. These reside chiefly in the leaf itself and especially in the complication introduced by the veins. Variations in turgor are a further source of error, as is also the actual technique of measuring thickness on leaves in position. If allowance be made for shrinkage, the simplest method is to make measurements on microtome sections from representative areas on which to base a range or average. The histological material obtained from the various series is yet to be worked up in connection with similar adaptations in native transplants, but a preliminary study of leaf thickness has been made for series V. The averages for each holard gradient in the four light intensities are in fair correspondence with the latter, the thickness falling rapidly from sun to 32 and 16 per cent. and then slightly to 8 per cent., *viz.*, 0.2923, 0.2462, 0.2016, and 0.2002.

Relative rôles of water and light

In all the series, it is obvious that water plays a considerable part in the elongation of stems and the expansion of leaves. This is naturally to be expected, chiefly on the basis of its mechanical action in turgor, but to some extent also because of its use as raw material, and this is supported by the

responses in both native and control cultures. More difficult of answer, however, is the question as to the respective importance of water and light in growth under reduced light intensities. Probably the frequent statement that plants stretch up in the shade in order to secure more light is intended to be more or less figurative, but the response is so graphic as to seem to lend support to this explanation. The major objective of the present investigation is to discover whether the relation to each of the factors permits quantitative expression.

TABLE IV

MAXIMUM DIFFERENCES BETWEEN EXTREMES

LIGHT EFFECTS			
HOLARD	STEM HEIGHT	DRY WEIGHT	LARGEST LEAVES
%	*cm.*	*gm.*	*cm.*^{2}
35	17.6	39.43	334
26	28.7	28.67	318
18	32.0	15.02	251
13	14.8	4.63	127
Average	23.3	22.19	257
LIGHT		HOLARD EFFECTS	
%	*cm.*	*gm.*	*cm.*^{2}
100	34.5	35.15	426
32	41.4	11.07	330
16	39.9	3.30	175
8	44.2	1.45	124
Average	40.0	12.74	264

The averages of the maximum differences for light and for water responses deviated little from each other in the case of the largest leaves, and this was true likewise of leaf area and stem diameter. However, both stem height and dry weight exhibited striking divergences. The maximum difference in stature produced by light within the various holards ranged from 14.8 to 32 cm., with an average of 23.3 cm., while for the holard gradient within each light set the respective values were 34.5 and 44.2 cm., with an average of 40 cm. Similarly, in the table for series V, the differences between the extreme averages for light intensities, namely, 37.2 and 58.5, is 21.3 cm., while for the four holards the corresponding figures are 64.7 and 26.4, with a difference of 38.3 cm. Hence, the excess of stature

in terms of response to water over that to light is 16.7 cm. in one case and 17 in the other. For all three series the difference between the greatest and least average height for the holard was 27.7 cm.; for light, it was 17.3 cm. On the basis of the average height for all series and conditions, the difference, 10.3 cm., amounted to 21 per cent. in favor of water.

With respect to the dry matter produced, the situation was reversed. The differences between extremes ranged from 4.63 to 39.43 gm. with an average of 22.19 gm. for light, to respective values of 1.45 to 35.15 gm. and an average of 12.74 gm. for water. For the three series, the difference between the highest and lowest averages was 12.33 gm. for water and 21.44 gm. for light. The excess to be ascribed to light is 8.9 gm., which approximates closely the average dry weight for all series and conditions, namely, 9.1 gm., and thus indicates that the rôle of light in producing construction material is twice as great as that of water. This relation is reflected in the production of photosynthate as measured by the picric acid method. From 8 per cent. light to full sunshine the amount rose from 0.384 to 1.408 mg. per $cm.^2$, a gain of 1.028 mg., while for the increase from 13 per cent. to 35 per cent. holard, the rise in sugars was but 0.45 mg. This was somewhat less than half as much, but the departure from the value derived from the dry weights is not serious.

From the foregoing, the conclusion seems warranted that variations in holard exert a minor effect upon the amount of material for the construction of stems while light plays the paramount rôle. On the other hand, the mechanical action of water is increased as the resistance offered by materials drops in proportion to photosynthesis. This would seem to find expression chiefly in the stem where the ratio between dry matter and sap-content is low by contrast with the leaf where the ratio is high. This is further indicated by the small differences in the averages for largest leaves and leaf areas (table IV). However, the results obtained during the past fifteen years in growing nearly a hundred species in lath-houses, length-of-day tents, in water and nutrient sequences, as well as a much larger number in transplant gardens, demonstrate that there may be considerable differences in behavior between species and genera as well as between life forms.

The major rôle assumed by the holard in the elongation of shoots serves to explain several apparent contradictions in the behavior of transplants, as well as of species subjected to factor gradients. At the outset it was expected that the transfer of alpine dwarfs from the summit of Pike's Peak to the plains at 6000 ft. or to the sea coast at Santa Barbara would produce an increase of stature. This did not happen in most cases and it was soon realized that this must be due to increased transpiration in the presence of a holard often tending toward a deficit. In short, the striking change of

climate had little or no effect upon elongation except during wet seasons, and to modify the dwarf habit effectively it became necessary to maintain an adequate water content. As to the prevalence of dwarfing in the alpine tundra itself, it had been earlier discovered that this was characteristic of climax and subclimax communities. Wherever disturbance reduced competition for water, as in the so-called "gopher gardens," or the supply was adequate as in wet meadows, the stature increased from two to fourfold, to equal that at much lower altitudes.

The controlling influence of water has also become more and more evident in natural shade gardens located in the spruce climax at 8000 ft. At the time of installation it was assumed that survival would be greater and modification more rapid than in transplanting into the sun, but the reverse often proved true, especially as to survival. This was found to be due to high interception of the frequent but light showers by the canopy and even more to the thick layer of needles and duff that decreased penetration to the root level. It was thought to cure this by sprinkling, but it finally became necessary to remove much of the duff to assure a proper water content. This accomplished, the shade gardens became the most prolific in striking modifications and pointed the way to the greater control and success achieved by means of lath-houses at the three altitudes.

Summary

Phytometer batteries of sunflowers have been employed in combinations of four degrees of holard with four of light to determine the respective rôles of these two factors in the apparent response to shade. The results obtained indicate that water assumes the major rôle in stem elongation, and light the larger part in the production of dry matter, the two necessarily cooperating in the adaptation characteristic of shady habitats.

THE ALPINE LABORATORY
CARNEGIE INSTITUTION OF WASHINGTON
MANITOU, COLORADO

Reprinted from PLANT PHYSIOLOGY, 10: 637–660, 1935.

FURTHER STUDIES OF ELONGATION AND EXPANSION IN *HELIANTHUS* PHYTOMETERS

FREDERIC E. CLEMENTS AND FRANCES L. LONG

Introduction

The investigation of the factors and functions involved in elongation and expansion under reduced light intensity has been continued with the special purpose of relating these to structural modifications as well as to growth forms. The ultimate objectives in these studies are to measure in terms of adaptation the climates and edaphic habitats characteristic of the various transplant gardens and to permit interpreting the functional responses of natives not susceptible of phytometer treatment. At the same time, opportunity was taken to increase the number of light values to six, in order to simulate the whole range of natural habitats, as well as the control conditions in the lath-houses. In addition, an inquiry was made into the effect of size of container, and a battery of free phytometers was installed in the soil under each light intensity in order to integrate all the direct factors of the six eces.

Methods

The several light values were secured by means of lath-huts 6 ft. high and 8×12 in section. These were constructed of standard plaster lath $1\frac{1}{2} \times \frac{3}{8}$ inches in section, which were so spaced as to produce approximately the five intensities desired. The relative spacing and light values were as follows: (1) spacing $4\frac{3}{4}$ in., intensity 65 per cent. of full sunshine; (2) spacing $1\frac{3}{4}$ in., intensity 44 per cent.; (3) $\frac{3}{4}$ in. apart, 27 per cent.; (4) $\frac{3}{8}$ in. apart, 19 per cent.; (5) $\frac{3}{16}$ in. apart, 11 per cent. These values were approximately the same as in the large lath-houses used for producing adaptations, but the lowest of these had a rating of but 6 per cent., thus yielding six conditions beside full sunshine. Each hut was provided with a door of the same construction and after serious experience with on-shore winds, was firmly anchored at the four corners. Provision was also made for raising the huts several feet to accommodate height growth in the higher intensities. To facilitate weighing the exceptionally large number of phytometers, a hut 12 ft. tall and 6 ft. in cross section was built nearby and this served also for photographic purposes.

A stopwatch photometer was employed to measure intensities, and readings were taken hourly in the sun and in each hut for representative days during the growing season. For the exposure, the photometer was carried

through a wide circle with a uniform motion in order to integrate as accurately as possible the alternating bands of sun and shade. While this procedure does not insure exact results, it is the best so far devised for lathhouse conditions. The many exposures were then evaluated by the usual standard and graphs were made for the intensity through the day for the various habitats, using time of day for the abscissa and percentage of light as the ordinate. By using a planimeter to integrate under the curves, the the respective values were obtained in terms of full sunlight as 100 per cent. From the averages of these were obtained the final values for each hut, these being the mean of the total radiation for the day.

Four sizes of containers were employed, the largest being garbage cans 25 in. high and 17 in. in diameter; the others were respectively $11 \times 8\frac{1}{2}$ in., 10×8 in., and 7×6 in. These three were of the more recent type with conical lids and apertures 2 in. across to accommodate stem and watering tube. The cans were sealed with a mulch of fine dry sand and above this the opening was closed by a band of non-absorbent cotton wrapped about the plant stem. As a special provision against sudden rainstorms, rubber aprons were cut from old inner tubes in the form of circles 12 cm. in diameter, with a hole 1 cm. wide in the middle and a slit running to the margin. When the apron was placed around the stem, the edges of the slit were overlapped and held in place by paper-clips at the outer and inner margins. Contact between rubber and stem was prevented by a thin band of absorbent cotton. The conical shape of the apron led away the rain that might drip down the stem and at the same time prevented injury to the latter, in addition to promoting aeration in some measure. When rains promised to be heavy, canvas covers were placed above the batteries as an additional safeguard.

The soil employed was a good loam of the same quality as in previous experiments and similar technique was used in filling the containers uniformly, as well as in planting the seeds and caring for the seedlings (3). The four holards were set respectively at 35, 26, 18, and 14 per cent. of the dry weight of the soil, and six containers of each value were assigned to each of the six light intensities. Five seeds were planted in each container and allowed to germinate, but when the plumules were well developed, one seedling closest to the measured average for the series was selected and the others carefully removed. No further selection was made in organizing the batteries for the various conditions, the cans merely being grouped in accordance with the numerical sequence. All sets were kept in the greenhouse until the seedlings were well established; this period was two weeks for the fall and three weeks for the spring series. As a consequence, some slight differentiation due to holard was apparent at the time the batteries were distributed to the six light intensities.

At the outset, the phytometers were weighed at weekly intervals; but as they grew larger, weighing necessarily became more frequent, first daily and finally three times a day. The amount of water lost was replaced after each weighing in order to maintain the holard as nearly uniform as possible. For this purpose, a 500-cc. burette was employed, the water being delivered to the plant through a tube reaching into the lower part of the container. To avoid any possibility of harmful accumulation of salts from the hard water of the locality, rain water was utilized throughout the series. Measurements of stem height and diameter and of leaf dimensions were taken on the same day and in the same order each week, thus yielding a cumulative record of growth for the entire period. In spite of the fact that the 14 per cent. holard was but 2 to 3 per cent. above the echard for the soil and that the 35 per cent. was practically at the limit for adequate aeration, frequent watering and rate of loss so nearly balanced each other that the tendency toward wilting or an aeration deficit was rarely in evidence. The generally uniform distribution of the water in the soil is reflected in the root systems, which were well distributed and not compacted about the inner surface of the can (fig. 1).

Function and growth responses

Two seasonal installations were employed in this investigation. The fall-winter series was planted October 16, the phytometers distributed to the lath-huts October 30, and the experiment terminated February 11, 1935. The spring series was begun February 28; all cotyledons were expanded by March 8, at which time the various holards were standardized. These batteries were placed in the several situations on March 21 and the final results were secured on June 4. The period of growth for the first series was 119; for the second, 97 days. In both cases the plan had been to follow the course of development to flowering and fruiting, but a heavy gale flattened the lath-huts and abruptly terminated the fall series, destroying the leaves but injuring the heads only slightly. While the spring series suffered no such mishap, the weather conditions of a marine climate and the behavior of such a warm-temperate species as the sunflower precluded maintaining the series until all heads were mature.

The interval between the time of flowering in the sun and in the lowest light intensity was so long that plants in the higher light values lost one-third or more of their leaves. Thus, the average number of leaves produced in the sun and 35 per cent. holard was 37.7 per plant, while by the end an average of but 27 leaves remained, the lower 10 having dried and disintegrated. In 44 per cent. light, the average loss was less, *viz.*, 7 out of 39; in 19 per cent. 3 in 27; and in 11 per cent. 1 out of 22. This inevitably led to a cumulative discrepancy in the photosynthesis and transpiration of

FIG. 1. Series of roots through the four holards and six light conditions.

TABLE I

AVERAGE OF MEASUREMENTS ON JUNE 4 FOR THE LARGE PHYTOMETERS

FACTOR GRADIENTS		STEM				H/D	LEAF AREA PER PLANT		LEAF NUMBER				TRANSPIRATION		WEIGHT OF PLANT			WATER REQUIREMENT	
LIGHT	HOLARD	HEIGHT		DIAMETER					TOTAL		JUNE 4		TOTAL	TOTAL	WET	DRY	DRY		
%	%	*cm.*	%	*cm.*	%		*sq. cm.*	%		%		%	*gm. per plant*	*gm./sq. cm.*	*gm.*	*gm.*	%	*cc./gm.*	%
100	35	138.5	100	2.30	100	60.4	5775.0	100.0	37.7	100	26.0	100	18533	3.21	627.1	127.7	100.0	145.3	100
	26	127.9	92	2.04	89	62.5	5180.3	89.8	36.0	95	25.3	97	15194	2.93	508.8	106.8	83.5	142.2	98
	18	111.1	80	1.74	76	63.9	4372.0	75.8	32.2	85	27.7	106	8674	1.83	383.0	67.9	53.1	127.7	88
	14	83.2	60	1.07	47	77.8	2574.0	44.6	26.3	70	22.3	86	4938	1.92	209.8	39.2	30.6	125.9	87
	Ave.	115.2	83	1.79	78	66.1	4475.0	77.6	33.0	88	25.3	97	11835	2.47	432.2	85.4	66.8	135.3	93
65	35	172.0	124	1.85	80	93.0	4626.0	80.1	38.0	101	28.5	110	18448	4.00	507.3	105.4	82.5	175.0	120
	26	135.0	97	1.73	75	78.0	3465.3	60.0	32.2	85	25.3	97	14525	4.20	380.5	79.8	62.4	182.0	125
	18	104.0	75	1.30	57	80.0	3560.3	61.6	29.0	77	22.7	87	9123	2.56	306.1	63.7	49.9	143.2	99
	14	85.2	62	1.10	48	77.5	3022.6	52.4	29.0	77	25.7	99	5322	1.77	230.7	39.9	31.2	133.4	92
	Ave.	124.0	90	1.49	65	82.1	3668.4	63.5	32.1	85	25.5	98	8223	3.14	356.2	72.2	56.5	158.4	109
44	35	191.0	138	2.13	93	89.6	7562.3	131.0	39.0	103	31.7	122	17562	2.32	577.6	105.5	82.5	166.4	115
	26	180.5	130	1.90	83	95.0	6884.0	119.2	31.7	84	25.5	98	13801	2.01	379.0	77.1	60.4	179.0	124
	18	137.0	99	1.40	61	97.9	5080.3	88.0	29.0	77	25.7	99	8529	1.68	308.6	59.1	46.3	144.3	99
	14	107.2	77	1.03	45	104.1	2984.3	51.6	29.3	78	26.0	100	4287	1.43	251.9	30.6	24.0	143.9	99
	Ave.	153.9	111	1.61	71	96.7	5627.7	97.4	32.3	86	27.2	107	11045	1.86	379.3	63.1	53.3	158.4	109

TABLE I.—(*Continued*)

Factor gradients		Stem				H/D	Leaf area per plant		Leaf number				Transpiration		Weight of plant			Water requirement	
Light	Holard	Height		Diameter					Total		June 4		Total	Total	Wet	Dry	Dry		
%	%	*cm.*	%	*cm.*	%		*sq. cm.*	%		%		%	*gm. per plant*	*gm./sq. cm.*	*gm.*	*gm.*	%	*cc./gm.*	%
27	35	186.0	134	1.71	74	108.8	9645.3	167.0	35.0	93	32.0	123	16435	1.70	499.5	61.8	48.4	265.9	183
	26	192.0	139	1.53	67	125.3	6814.3	117.9	33.0	88	29.7	114	10515	1.55	358.4	57.6	45.1	182.8	126
	18	151.0	109	1.40	61	107.9	4676.3	81.0	30.3	80	28.0	108	6347	1.36	245.6	35.3	27.6	179.8	124
	14	101.7	73	1.03	45	98.6	2901.3	34.7	28.0	74	25.3	97	3672	1.83	143.2	20.6	16.1	178.2	123
	Ave.	157.7	114	1.42	62	110.1	5784.3	100.2	31.6	84	29.0	111	9242	1.61	311.7	43.8	34.3	201.7	139
19	35	200.0	144	1.56	58	128.0	5343.0	92.6	27.6	73	24.6	95	7512	1.41	295.0	24.9	19.5	301.5	208
	26	161.9	117	1.26	55	128.1	3613.1	62.6	27.0	72	25.7	99	4800	1.33	191.2	17.8	13.9	269.6	185
	18	141.0	102	1.00	44	141.0	2628.7	45.5	27.0	72	24.3	93	3538	1.35	133.3	15.9	12.4	222.5	153
	14	102.5	74	.83	36	123.3	1776.6	30.8	25.0	66	22.3	86	2108	1.19	83.5	11.2	8.8	188.2	130
	Ave.	151.3	109	1.16	48	130.1	3440.3	57.9	26.7	71	24.2	94	4490	1.32	175.7	17.5	13.7	245.4	169
11	35	139.0	100	1.13	49	123.0	2279.0	39.4	21.3	82	22.3	59	3018	1.33	96.3	7.5	5.9	402.5	277
	26	130.6	94	1.00	44	130.6	1491.6	25.8	19.6	75	22.3	59	1888	1.27	65.2	5.3	4.2	356.2	245
	18	113.5	82	0.83	36	136.8	1390.5	24.1	21.3	82	21.3	56	1637	1.18	55.8	5.3	4.2	308.8	212
	14	76.0	55	0.70	30	108.6	792.9	13.7	20.0	77	23.6	60	620	.78	37.4	2.9	2.3	213.8	147
	Ave.	114.7	83	0.91	40	124.7	1488.5	25.7	20.5	79	22.4	58	1791	1.14	63.7	5.3	4.1	320.3	220

the several light batteries, and necessitated closing the experiment before the buds opened in the weaker light intensities. In spite of its many advantages, which are distinctly greater than those of any other species so far utilized for standard phytometers, *Helianthus annuus* possesses the two defects of blocking off the lower leaves and of growing slowly in cold seasons such as that of 1934–1935 at Santa Barbara, as also in the climate of the alpine tundra on Pike's Peak.

The results for transpiration and water requirement, as well as for growth in terms of stem, leaf, and dry weight, were in close accord for the two series. The agreement between these and the five series discussed in the previous paper was likewise striking. Since in the present experiment there were six light intensities instead of four, the detailed results are given for light: holard in table I and these are summarized in the next paragraph. The weights were also determined separately for stem, leaves, roots, and heads, as shown in table II. In addition, a comparison is made between the results obtained from the four sizes of containers, not merely in connection with the two series, but also to throw light upon the phytometer method itself.

Under each light intensity, stem height was greatest in 35 per cent. holard and decreased consistently with the reduction to 14 per cent., with a single exception, the maximum of 200 cm. falling at 19 per cent. light and 35 per cent. water content (fig. 2). The greatest average height for the four holards occurred in 27 per cent. light, but 44 and 19 per cent. yielded values only a little less, while the shortest stems were found in sun at 115.2 cm. and 11 per cent. light at 114.7 cm. The diameter of the stem fell off steadily from 35 to 14 per cent. holard in every battery, ranging from the maximum of 2.3 cm. in the sun to 1.13 cm. in 11 per cent. light intensity. The average for each light value decreased from 1.79 cm. in the sun to 0.91 cm. in the deepest shade, that for 65 per cent. light being in disagreement here as in some other places, owing to leakage in a few containers during a heavy rain.

The total leaf area per plant diminished from 35 to 14 per cent. with great regularity, the one exception occurring at 65 per cent. light and 26 per cent. holard. However, the maximum was at 27/35 per cent. with a value of 9645.3 sq. cm. and the minimum of 792.9 at 11/14 per cent., a ratio of approximately 1:12. The highest average was found in 27 per cent. light, followed closely by 44 per cent.; the average area in the sun was three times greater than that for the lowest light intensity. The total number of leaves produced dropped regularly with the holard for the first four light intensities, but was almost constant for the two lower values, the range being from 39 to 21. The average number for each battery fell from 33 in the sun to 22 at 11 per cent. The number of leaves present at the close

TABLE II

WET AND DRY WEIGHTS OF PLANT PARTS FOR THE SPRING SERIES

FACTOR GRADIENTS		WET WEIGHT					DRY WEIGHT				
LIGHT	HOLARD	STEM	LEAVES	ROOT	FLOWER	TOTAL	STEM	LEAVES	ROOT	FLOWER	TOTAL
%	%	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
100	35	364.5	128.8	125.7	25.8	644.8	83.8	24.4	34.7	5.30	148.20
	26	313.0	145.8	125.7	14.0	598.5	73.7	26.1	19.4	2.73	121.90
	18	207.8	116.5	53.5	5.4	383.2	34.3	19.5	7.8	1.11	62.70
	14	113.0	69.1	32.0	14.2	228.3	18.4	11.6	4.0	2.62	36.60
	Ave.	249.6	115.1	84.2	14.8	463.7	52.5	20.4	16.5	2.94	92.30
65	35	337.8	88.6	70.0	8.8	505.2	74.5	19.4	21.6	2.13	117.63
	26	250.0	66.8	49.2	2.5	368.5	52.7	12.3	12.6	0.60	78.20
	18	100.7	46.8	44.5	70.0	262.0	24.7	10.2	7.7	14.96	57.50
	14	61.7	34.1	29.8	64.1	189.7	11.8	7.1	3.5	11.70	34.10
	Ave.	187.5	59.1	48.4	36.7	331.3	40.9	12.2	11.4	7.35	71.86
44	35	453.9	120.8	79.5	17.5	671.7	83.8	29.1	16.7	3.73	133.33
	26	284.1	124.5	41.2	28.1	477.5	50.9	22.3	9.7	5.70	88.60
	18	132.5	75.5	42.3	54.9	305.2	28.4	15.9	6.4	11.80	64.50
	14	89.7	43.5	25.8	25.7	184.7	15.0	10.8	2.1	5.00	32.90
	Ave.	240.1	91.1	47.2	31.6	409.7	44.5	19.5	9.0	5.43	79.83
27	35	342.3	121.2	51.5	1.2	516.2	36.9	18.1	9.5	0.44	64.94
	26	258.2	100.0	23.6	2.5	384.3	36.8	16.3	7.5	0.66	61.26
	18	154.2	58.5	11.0	8.1	231.8	20.0	10.7	3.1	1.75	35.50
	14	87.0	43.9	9.2	2.1	142.2	10.0	7.0	3.1	0.55	20.65
	Ave.	210.4	80.9	23.8	3.5	318.6	25.9	13.0	5.8	0.60	45.83

TABLE II.—(*Continued*)

Factor gradients		Wet weight					Dry weight				
Light	Holard	Stem	Leaves	Root	Flower	Total	Stem	Leaves	Root	Flower	Total
%	%	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
19	35	206.0	50.7	8.3	.0	265.0	16.7	8.5	1.5	0.13	26.83
	26	125.0	28.0	8.0	.0	161.0	11.0	4.4	1.5	0.30	17.20
	18	84.8	18.6	4.3	.0	107.7	8.6	3.2	1.0	0.30	13.10
	14	48.8	19.5	4.4	.6	73.3	5.8	3.3	1.4	0.22	10.72
	Ave.	116.2	29.2	6.3	.6	151.9	8.4	4.9	1.4	0.24	16.96
11	35	79.7	20.0	3.7	0	103.4	4.6	2.6	0.72	0	7.92
	26	50.0	11.0	1.7	0	62.7	3.1	1.9	0.32	0	5.32
	18	38.2	10.2	2.0	0	50.4	2.0	2.4	0.52	0.04	4.95
	14	16.5	6.3	1.0	0	23.8	1.3	1.1	0.30	0.03	3.03
	Ave.	46.1	11.9	2.1	0	60.1	2.7	2.0	0.46	0.04	5.31

was greatest in the intermediate light values, namely, 29 at 27 per cent. and 27 at 44 per cent., and least in 11 per cent. However, the highest average loss of leaves was 8 in the sun, falling to 7, 5, 2.5, and 2 at 11 per cent.

With respect to total transpiration per plant, the descending order was entirely consistent with the reduction in holard. In the first three light

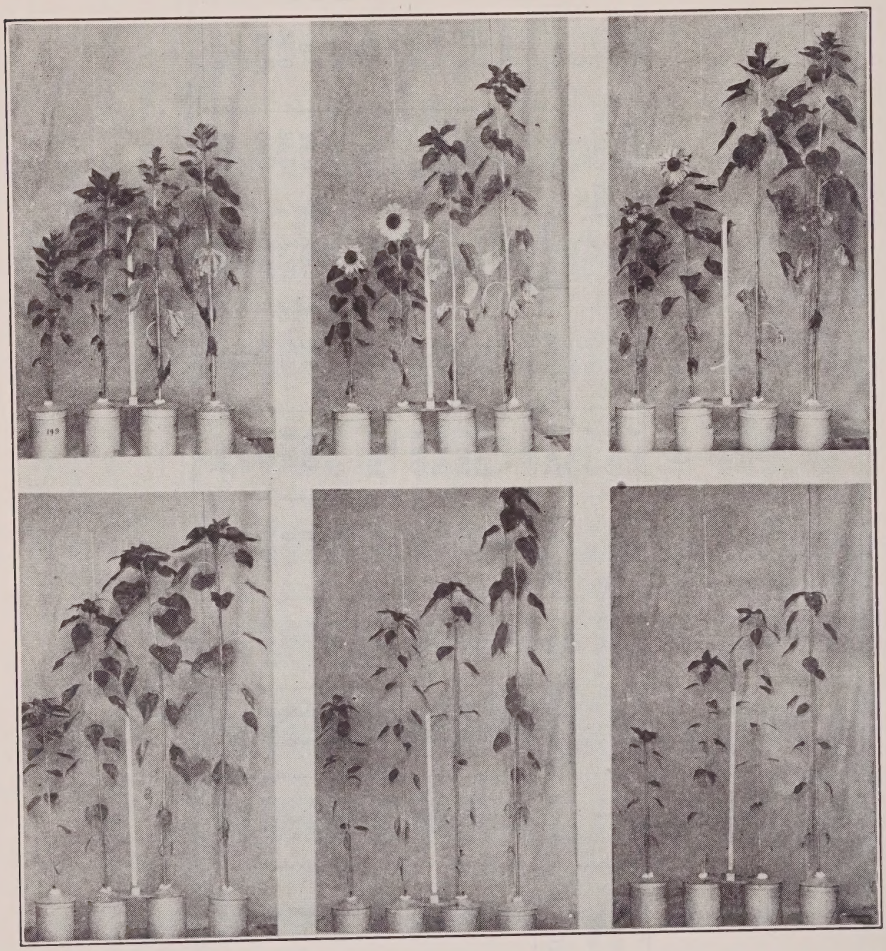

FIG. 2. Representative phytometer sets from each light habitat, arranged according to holards 14, 18, 26, and 35 per cent.

values the loss in 35 per cent. holard was nearly four times as great as in 14 per cent., and in 11 per cent. light, five times as much. The average loss for each light battery was in accord with diminished intensity, except for 65 per cent., as just explained. The loss in grams per sq. cm. decreased with the holard with fair regularity, while it agreed with the light intensity,

with the exception of 65 per cent. again. As a rule the water requirement was highest in the holard of 35 per cent., with two slight exceptions for 26 per cent., and uniformly lowest in 14 per cent. The average water requirement rose consistently with reduced light from 135.3 cc./gm. for sun to 320.3 cc./gm. for the lowest light value, apart from the same figure for 65 and 44 per cent.

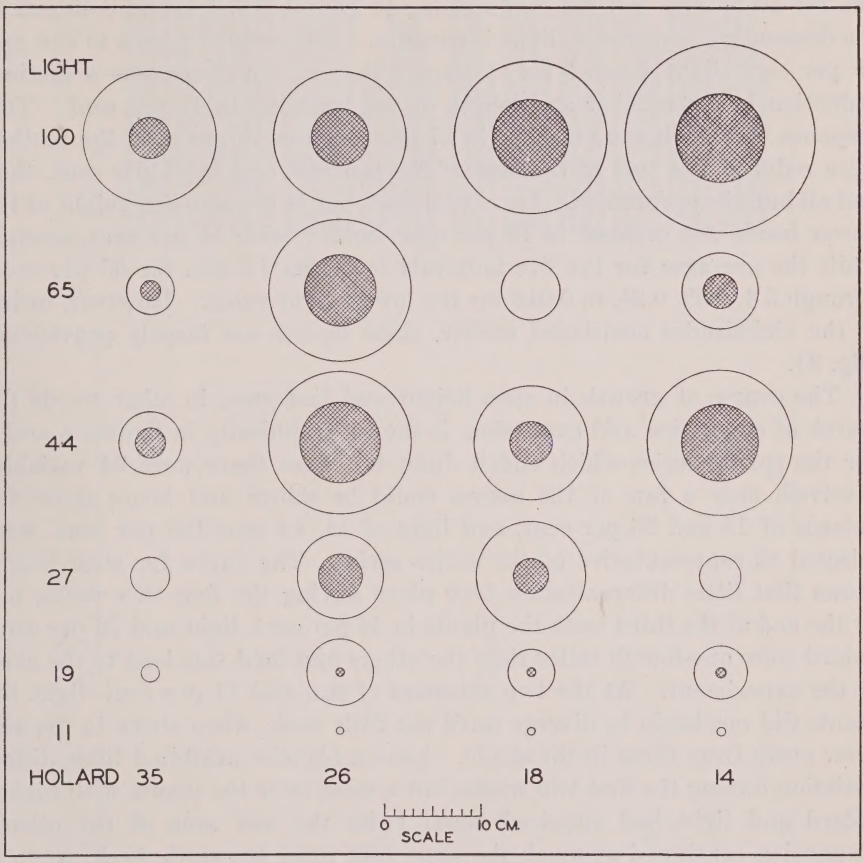

FIG. 3. Comparative diagram of flower heads; disk cross-hatched, rays plain, buds clear.

Wet weight of plant exhibited a complete correspondence with holard, falling off with much uniformity from 35 to 14 per cent., while the dry weight was equally consistent. This was likewise true for the averages, the respective values for the six light intensities from sun being 85.4, 72.2, 63.1, 43.8, 17.5, and 5.3 gm. When the organs of the plant were weighed separately, the wet weight of the stem decreased consistently, as did that of leaves and roots with but one or two slight discrepancies. The dry weights of all three gave similarly accordant results, the maximum of 83.8 gm. for

the stem falling in 100/35 per cent. and the minimum, 1.3 gm., in 11/14 per cent., the averages for the light extremes being 52.5 and 2.7 gm. The maximum for the leaves was 29.1 and the minimum 1.1 gm., with the average for the sun 20.4 gm. and for 11 per cent. light, 2 gm. The highest value for roots fell at 35 per cent. holard in sun, namely, 34.7 gm., while the lowest, 0.3 gm., was found at 11/14 per cent. The average weight was 16.5 gm. for all holards in the sun, dropping to 11.4, 9, 5.8, 1.4, and 0.46 gm. in the descending sequence of light intensities. The roots of plants in sun and 65 per cent. light formed very compact masses, but there was a distinct reduction in the number and length of the branches in 44 per cent. This response was much more marked in 27 per cent.; in 19 per cent. the rootlets were reduced to a tuft at the base of the tap root and in 11 per cent. they had all but disappeared (fig. 1). In all cases but in the sun, the weight of the flower heads was greatest in 18 per cent. holard, with 14 per cent. second; while the averages for the five lath-huts fell from 7.3 gm. for 65 per cent. through 5.4, 0.59, 0.24, to 0.018 for the lowest light value. However, owing to the vicissitudes mentioned earlier, these figures are largely provisional (fig. 3).

The course of growth in stem height and leaf area, in other words the march of elongation and expansion, is shown graphically in figures 4 and 5 for the spring series which ended June 4. Since there were 24 variables involved, only a few of the curves could be shown and hence those for holards of 14 and 26 per cent. and light of 11, 44, and 100 per cent. were selected as representative of the entire series. The curve for stem height shows that little differentiation took place during the first two weeks, but by the end of the third week the plants in 44 per cent. light and 26 per cent. holard were one-fourth taller than the others and held this lead to the close of the experiment. At the two extremes of sun and 11 per cent. light the plants did not begin to diverge until the fifth week, when stems in the sun drew away from those in the shade. Leaves likewise exhibited little differentiation during the first two weeks, but a week later the plants with higher holard and light had acquired about twice the leaf area of the others. Expansion continued at much the same rate until the sixth week, when it became definitely greater for the 44 per cent. light. The lowest holard counterbalanced higher light values and the individuals in sun and 44 per cent. light did not diverge until the ninth week.

The influence of size of container was made the subject of a special inquiry, which took account of free phytometers as well as the four types of can indicated earlier. The standard container when complete weighed 15 kg., the intermediate 12 kg., and the smallest 4.5 kg., while the garbage cans reached a total of 110 kg. when filled. The latter were employed as controls, chiefly for the batteries of free phytometers which could not be

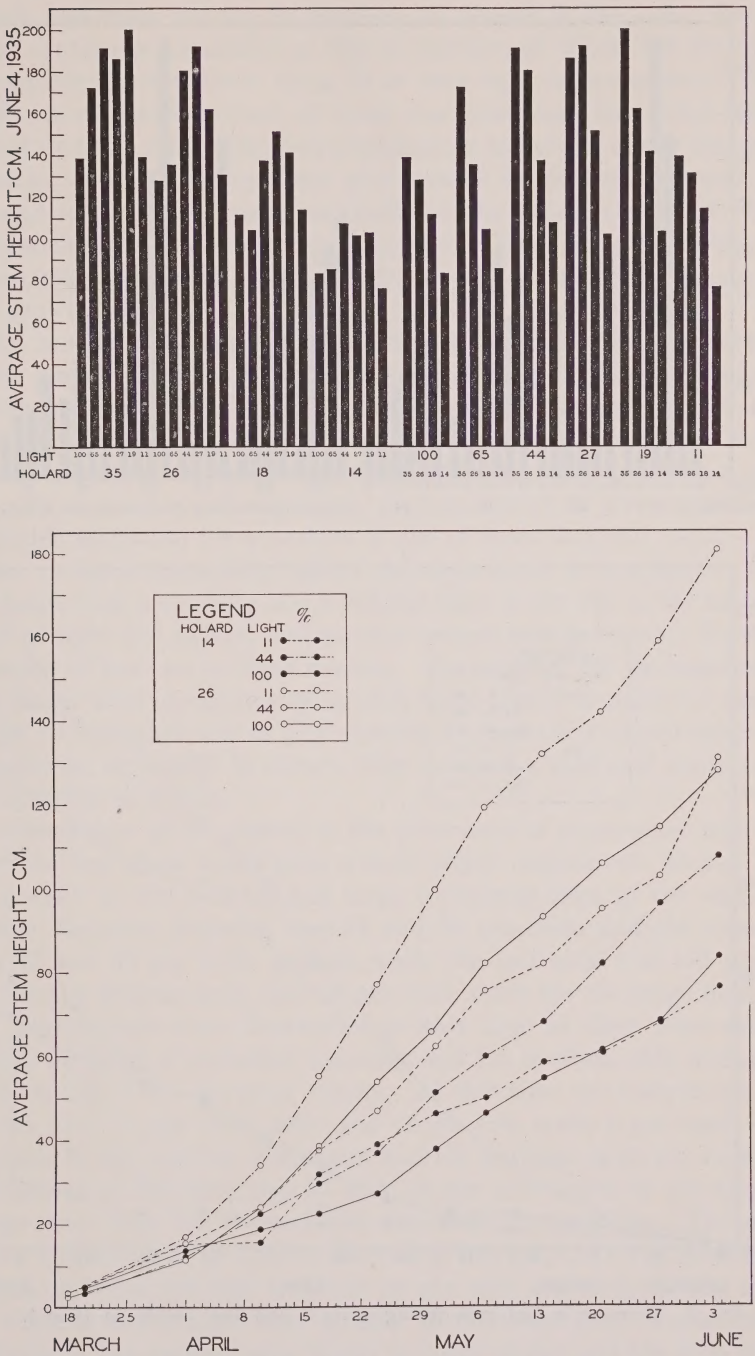

FIG. 4. March of average stem height for series 2, and final values on June 4.

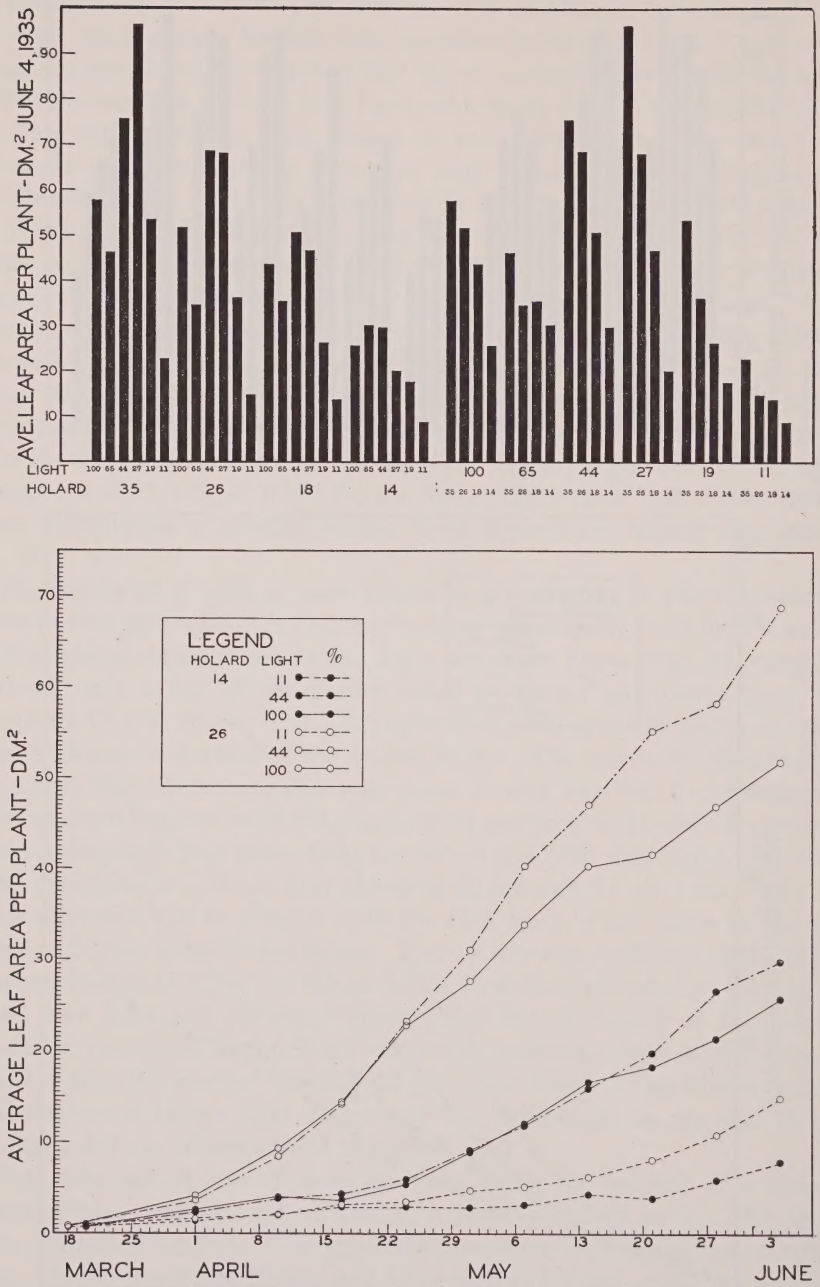

FIG. 5. Increase in leaf area during series 2, and final values on June 4.

weighed, and were but six in number, all placed in the sun. The three sizes of containers amounted to 348 in number, of which 148 belonged to the large phytometer, there being 24 in each light intensity and 6 in each holard. A measured amount of water was given each day, after they had attained a certain size, to the free phytometers in the soil under the six light conditions, and the garbage cans were treated in the same manner. This amounted to giving both sets practically all the water they could use; this fact probably has some bearing upon their slower growth at first when aeration may well have been a factor, as well as upon their much more rapid growth later.

As a consequence, no strict comparison can be made between the growth of these plants and those in the standard containers. They do confirm the experience derived from many phytometer series through two decades to the effect that number and size of container must always be balanced against each other. With 24 sets of conditions, as in the 9 series that have dealt with elongation and expansion, phytometers of 15 kilos. constitute the practicable maximum for a number of 200 or more that will require weighing two to three times daily before the experiment is completed. On the other hand, such a capacity sets a definite limit to growth in the better conditions of light and holard, and phytometers of this size have a dependable life period of but two to three months. By contrast, the garbage-can type of the larger sizes permits carrying such large plants as sunflower and corn through to maturity, but as phytometers to measure a considerable range of conditions, especially in nature, they demand a staff and equipment all but impossible to realize.

A comparison of the growth in the three sizes of phytometer cans at the end of the first three weeks gave a stem height respectively 35 and 40 per cent. greater in the medium and large containers than in the small ones. Likewise, the stem diameter was 21 and 35 per cent. and the number of leaves 40 and 50 per cent. greater, while the leaf area was 133 per cent. more for the medium cans and 52 per cent. more for the large ones. The small phytometers were dismantled at this time as they were evidently reaching the limit of container capacity, and the medium ones were discontinued on May 1 for the same reason. At this time the individuals of the large set were 11 per cent. taller and of the free series 9 per cent. shorter than those in the medium containers and the garbage cans, but in contrast the diameter of the stem was 19 and 14 per cent. more in the large and garbage cans than for the medium and free phytometers. The average number of leaves was 21 for the three sets, but only 14.6 for the free phytometers, in which the leaf area was 24 per cent. less than for the medium cans, while it was 2–4 per cent. greater in the other two. From this time the plants in the garbage cans began to forge ahead and the free phytom-

eters to grow more rapidly than those in the large cans. At the end of the experiment on June 4, the relative values were as follows for the large, free, and garbage-can phytometers: stem height 100, 116, 136; stem diameter 100, 131, 167; number of leaves 100, 128, 149; leaf area 100, 237, 429.

The remaining three sets were taken off to permit determining wet and dry weights at the end of 12 weeks, with the results shown in table III.

TABLE III

WET AND DRY WEIGHTS OF THE THREE FINAL SETS

	PERCENTAGE LIGHT					
	100	65	44	27	19	11
	WET WEIGHT					
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Large cans	627.1	507.3	577.6	499.5	295.0	96.3
Free phytometers	1394.9	1265.5	1239.6	323.4	142.6	29.6
Garbage cans	2340.8					
	DRY WEIGHT					
Large cans	127.7	105.4	105.5	61.8	24.9	7.5
Free phytometers	204.8	168.7	127.9	43.7	13.8	2.0
Garbage cans	438.3					

For both wet and dry weights, the values for the garbage-can controls were approximately twice as high as for the free phytometers, and for these about twice as great as for the large phytometers, in the case of sun conditions. Both of the latter fall off consistently in weight with decreasing light intensity, and most rapidly in the lower intensities. The large cans begin to exceed the free plants at 27 per cent. light and both wet and dry weights are more than three times greater in 11 per cent. The cause of this reversal in behavior requires further investigation, as does also the striking difference in the three sets in the sun. This bespeaks better conditions in the larger soil masses, partly to be explained by the generous watering, and the drop in the free phytometers is most plausibly explained by the effect of this upon air content in the three lower light values.

Structural modifications

In addition to the striking responses in growth and form of stem, leaf, and roots, corresponding or compensating adaptations occurred in the intimate structure of these organs. These were especially exhibited by the stomata, as seen in tables IV and V.

The epidermis was stripped from the leaf and immediately placed in absolute alcohol in accordance with the usual technique, a median leaf being selected in each of the 24 sets. The strips were taken from the proximate

TABLE IV

NUMBER OF STOMATA PER SQ. MM. IN UPPER AND LOWER EPIDERMIS THROUGHOUT THE LIGHT AND HOLARD SERIES

LIGHT	HOLARD 35 PER CENT.		HOLARD 26 PER CENT.		HOLARD 18 PER CENT.		HOLARD 14 PER CENT.		AVERAGE NUMBER	
	LOWER	UPPER	LOWER	UPPER	LOWER	UPPER	LOWER	UPPER	LOWER	UPPER
%										
100	315	288	341	280	258	240	248	240	290.8	262.1
65	293	286	221	221	228	218	203	195	236.2	230.1
44	165	174	180	184	195	195	180	190	180.1	185.9
27	120	129	145	146	142	147	135	140	135.5	140.5
19	105	120	116	125	165	165	131	135	129.4	136.4
11	90	116	90	117	95	112	123	138	99.6	120.8
Ave.	182	186	182	179	181	180	170	173	178.6	179.3

center of the leaf, about halfway from the base to tip and from midrib to margin. The major correlation in number of stomata is with light intensity, the decrease from 100 to 11 per cent. being all but entirely consistent for both lower and upper surfaces in each holard and perfectly so for the averages of each light value (fig. 6). These range from 291 in 100 per cent. to 99 in 11 per cent. for the lower epidermis and 262 and 120 for the upper. The averages for the four holards are not significant except in the 14 per cent., since averaging obscures the most novel point in the behavior as to number. This is the fact that stomata are most numerous in the lower epidermis for 100 and 65 per cent., but tend to become slightly more abundant in the upper for the next two intensities and definitely so in the two

TABLE V

SIZE OF STOMATA IN MICRONS FOR THE LOWER EPIDERMIS OF PLANTS THROUGHOUT THE SERIES

LIGHT	HOLARD 35 PER CENT.	HOLARD 26 PER CENT.	HOLARD 18 PER CENT.	HOLARD 14 PER CENT.	AVERAGE SIZE
%	μ	μ	μ	μ	μ
100	34.4 × 24.1	20.1 × 24.8	31.8 × 23.7	28.3 × 21.2	28.7 × 23.5
65	24.7 × 24.1	32.9 × 23.4	23.8 × 21.2	28.3 × 21.2	27.4 × 22.5
44	31.8 × 21.2	34.3 × 22.3	28.3 × 21.2	26.6 × 21.2	30.6 × 21.5
27	33.3 × 26.6	33.6 × 21.2	30.4 × 23.4	28.3 × 21.2	31.4 × 23.1
19	33.6 × 24.8	31.8 × 24.8	31.2 × 21.6	30.1 × 21.2	31.7 × 23.1
11	34.0 × 24.4	31.8 × 24.8	29.4 × 23.0	28.3 × 21.2	30.9 × 23.4
Ave.	32.0 × 24.2	31.6 × 23.6	29.1 × 23.0	28.3 × 21.2	30.0 × 22.8

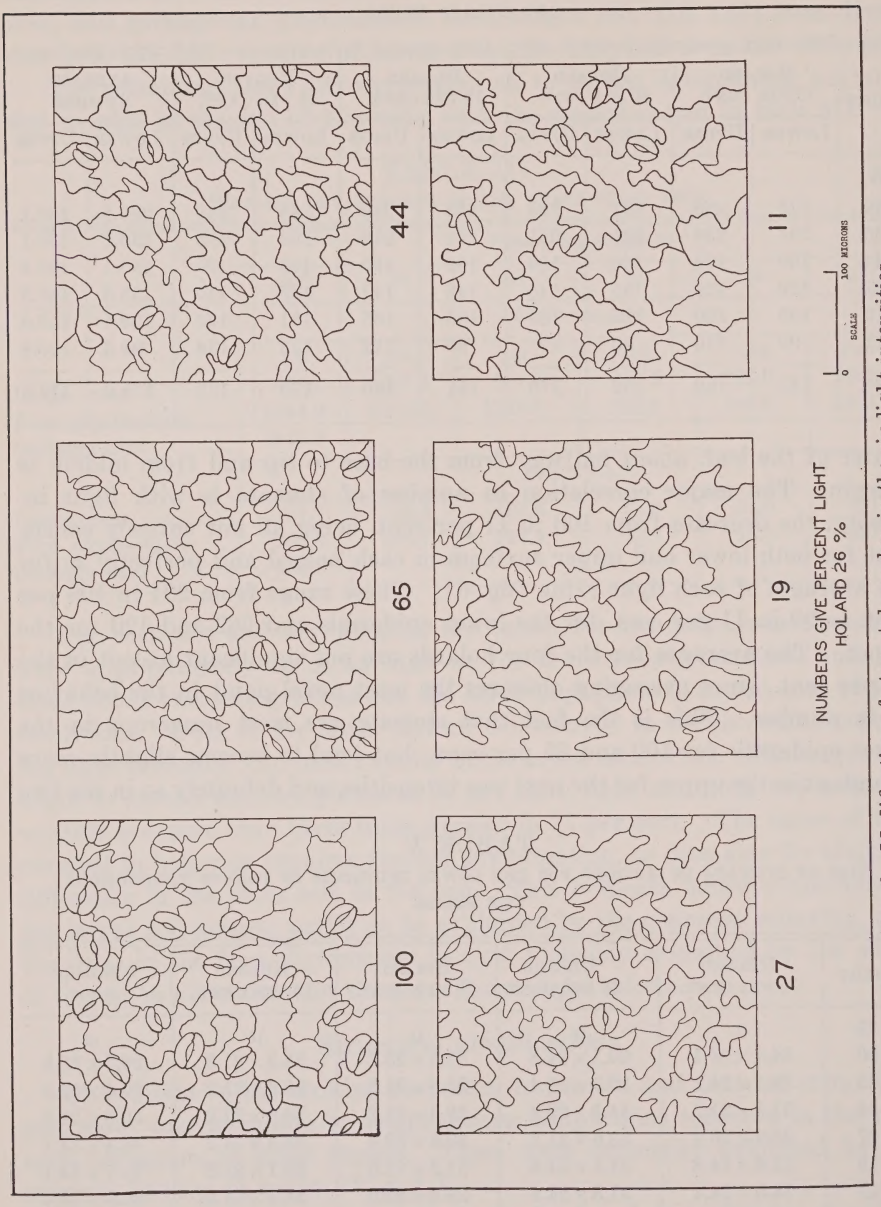

FIG. 6. Modification of stomatal number in the six light intensities.

lower values. While the numbers generally follow the relative expansion of the leaf, the change in preponderance from lower to upper surface makes it clear that the number of stomatal initials varies under the several conditions, not merely between surfaces but also between leaves and to a considerable extent independent of the degree of expansion.

Modification in size bears no evident relation to light intensity in any particular holard, but the average size for the three higher intensities is distinctly less than for the three lower ones. The chief difference, however, is to be found in the averages for the respective holards, the largest size occurring in 35 per cent. and this diminishing regularly to 14 per cent.

Quantitative changes in the mesophyll are reflected in the thickness of leaf, while the qualitative ones naturally affect the mesophyll, either as direct responses to light and water or indirectly in relation to stomata and air passages. As may be seen in table VI, the thickness of the leaf was

TABLE VI

THICKNESS OF LEAF, PALISADE AND SPONGE TISSUES

FACTOR GRADIENTS		LEAF	PALISADE	SPONGE
LIGHT	HOLARD			
%	%	μ	μ	μ
LARGE CANS				
100	35	267	153	114
	14	192	111	81
65	35	248	142	106
	14	177	106	71
11	35	142	96	46
	14	142	78	64
FREE PHYTOMETERS				
100	35	238	131	107
65	35	230	126	104
44	35	202	128	74
27	35	156	92	64
19	35	149	78	71
11	35	149	89	60
GARBAGE CANS				
100	35	258	135	124

greatest for the large cans in sun and 35 per cent. holard, followed in order by garbage cans, large can in 65/35 per cent., and free phytometers in sun and 35 per cent. The general agreement between the large and free phytometers was close, the two falling off consistently and in much the same

degree from a maximum in sun to a minimum in 11 per cent. light. For the large plants, 35 per cent. holard produced a leaf one-third thicker than 14 per cent., except for the lowest light intensity, where the values were the same. In this set the values for palisade and for sponge decreased

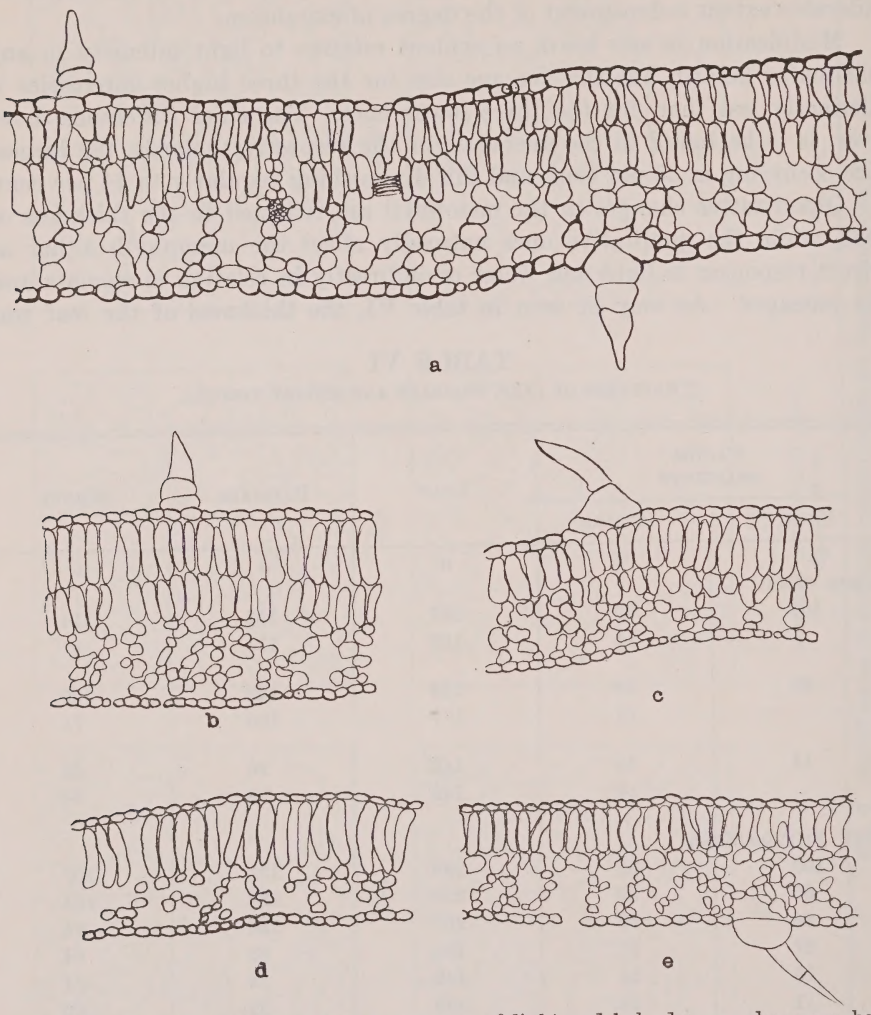

FIG. 7. Structure of mesophyll in extremes of light and holard: *a*, garbage-can battery; *b*, *c*, 65 per cent. light, 35 and 14 per cent. holard; *d*, *e*, 14 per cent. light, 35 and 14 per cent. holard. ×150.

regularly with reduced light, except for 11 per cent., and with this same discrepancy, each tissue was thicker in 35 per cent. than in 14 per cent., in accord with the behavior of the leaf itself. The free phytometers were somewhat less harmonious, but there was general reduction from sun to 11 per cent. light.

The mesophyll likewise exhibited structural modifications in close correlation with the factor dosage, as illustrated in figure 7. With the cross section of a median leaf from a garbage-can phytometer as the standard, a large-phytometer leaf from 65/35 per cent. agrees in having two full rows of palisade cells and essentially the same type of sponge tissue. However,

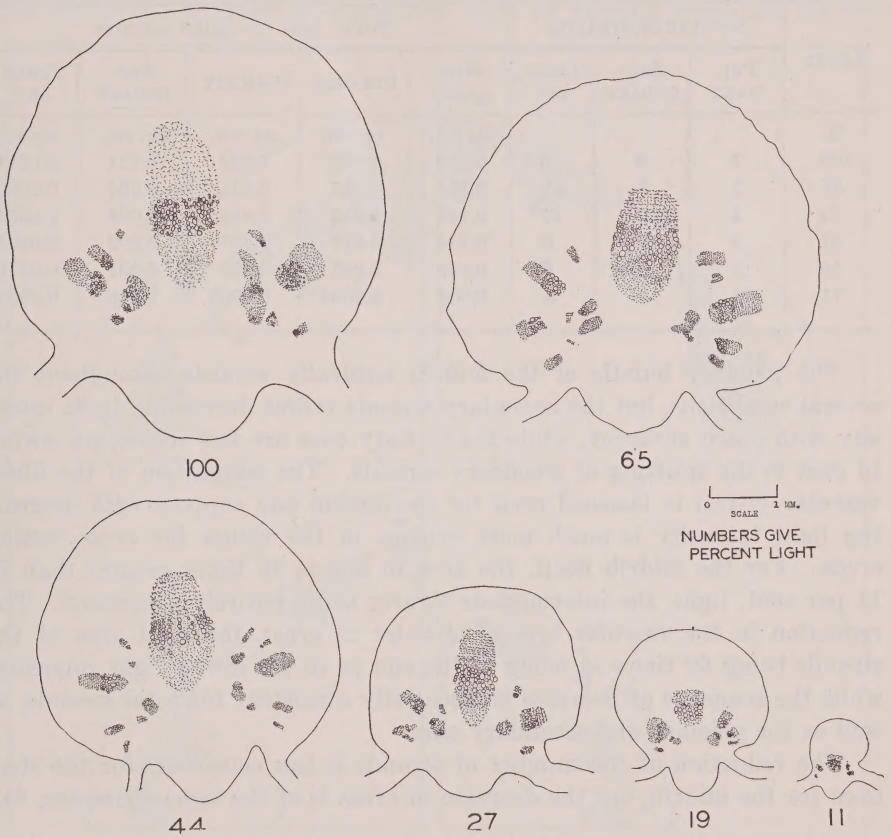

FIG. 8. Diagram of midrib in cross section, showing modification of fibrovascular system; 26 per cent. holard.

leaves in the same light intensity but in 14 per cent. holard had reduced the inner palisade cells to about half the length and the sponge also in some measure. In 11/35 per cent., the inner row of palisade had completely disappeared and the sponge tissue was much looser in texture, while 14 per cent. holard in the same light produceed a shorter outer row of palisade, with the inner reduced to globoid cells.

Cross sections of representative portions of the midrib were employed for comparison of the modification of the conductive-supportive tissues. These differences are best appreciated in the graphic form (fig. 8), but

an effort has been made to express them in quantities also, as shown in table VII.

TABLE VII

MODIFICATION OF THE FIBROVASCULAR SYSTEM IN MIDRIB; 26 PER CENT. HOLARD

LIGHT	NUMBER OF STRANDS			TOTAL AREA IN CROSS SECTION				
	PRIMARY	SECONDARY	TERTIARY	MIDRIB	STRANDS	PRIMARY	SECONDARY	TERTIARY
%				*sq. cm.*	*sq. cm.*	*sq. cm.*	*sq. cm.*	*sq. cm.*
100	1	4	6	0.268	0.036	0.022	0.011	0.0021
65	1	3	11	0.218	0.023	0.014	0.004	0.0055
44	1	2	13	0.147	0.022	0.014	0.003	0.0054
27	1	2	6	0.074	0.011	0.007	0.002	0.0023
19	1	1	6	0.039	0.005	0.002	0.001	0.0012
11	1	0	4	0.008	0.0006	0.0005	0.000	0.0001

The primary bundle of the midrib naturally persists throughout the several conditions, but the secondary strands reflect decreasing light intensity with much accuracy, while the tertiary ones are less consistent, owing in part to the splitting of secondary strands. The adaptation of the fibrovascular system to lessened need for conduction and support with decreasing light intensity is much more evident in the values for cross section areas. For the midrib itself, the area in sun is 30 times greater than in 11 per cent. light, the intermediate figures being entirely consistent. The reduction in the vascular system is twice as great, the total area of the strands being 60 times as much in the sun as in the lowest light intensity, while the sequence of decrease is essentially consistent for total strands, as well as for primary and secondary ones.

The reduction of the number of strands is less consistent for the stem than for the midrib, but the decrease in areas is of the same character, fol-

TABLE VIII

MODIFICATION OF FIBROVASCULAR SYSTEM OF STEM; 26 PER CENT. HOLARD

LIGHT	NUMBER OF STRANDS		TOTAL AREA IN CROSS SECTION	
	PRIMARY	SECONDARY	STEM	STRANDS
%			*sq. cm.*	*sq. cm.*
100	12	8	0.95	0.198
65	10	6	1.18	0.200
44	10	6	0.88	0.117
27	11	9	0.43	0.062
19	6	6	0.27	0.018
11	8	6	0.1	0.011

lowing the light intensity closely, with the exception of a small discrepancy in 65 per cent. (fig. 9). Moreover, while the stem area at 11 per cent. is seven times smaller than for the sun, that of the strands is 18 times less, or more than twice as much. In general the stem appears to be somewhat more plastic than the midrib, and this assumption is supported by the fact that under the pressure of continuous wind of varying velocities, bundles

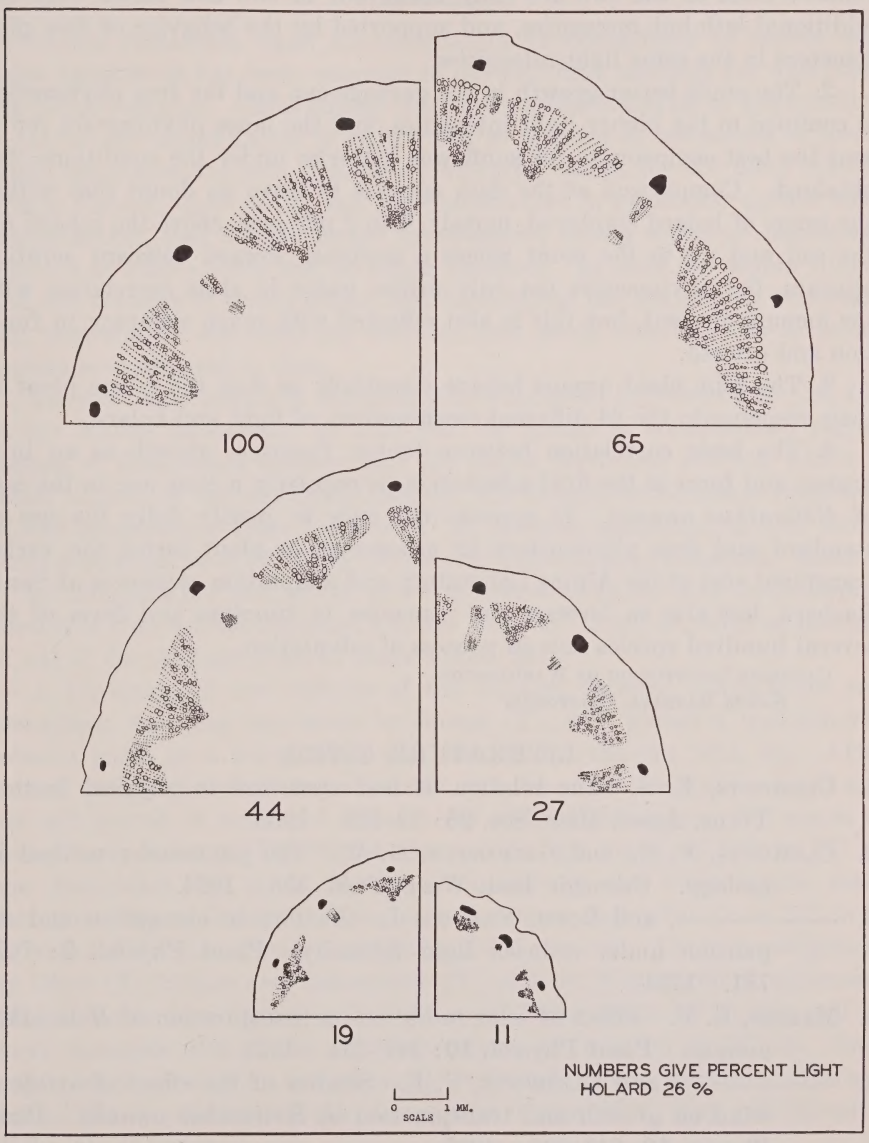

FIG. 9. Diagram of stem quadrants in cross section showing modification of fibrovascular system.

increase in number relatively more rapidly than in size and the bast strands receive special emphasis.

Summary

1. The conclusions reached heretofore as to the functional and growth responses of *Helianthus annuus* to combinations of light and holard and the relative rôles of the two are fully borne out in two new series with two additional lath-hut intensities, and supported by the behavior of free phytometers in the same light intensities.

2. The much better growth in the garbage-can and the free phytometers is confined to the higher light intensities, and the large phytometers represent the best compromise for sunflower batteries under the conditions that obtained. Comparison of the data appears to leave no doubt that within the range of holard employed, namely, 1 to 2 per cent. above the echard for the soil and up to the point where a tendency toward deficient aeration appears, the phytometers not only utilize water in close correlation with the amount present, but this is also reflected with much accuracy in function and growth.

3. The four plant organs behave essentially as does the entire plant in their response to the 24 different combinations of light and holard.

4. The basic correlation between factor, function, growth as an integrator, and form as the final adaptation, is regularly a close one in the case of *Helianthus annuus*. It appears not only to justify fully the use of standard and free phytometers in measuring in plant terms the varied transplant eces at the Alpine Laboratory and adaptation sequences at Santa Barbara, but also to forecast the responses in function and form of the several hundred species now in process of adaptation.

CARNEGIE INSTITUTION OF WASHINGTON
SANTA BARBARA, CALIFORNIA

LITERATURE CITED

1. CLEMENTS, E. S. The relation of leaf structure to physical factors. Trans. Amer. Micr. Soc. **26**: 19–102. 1905.
2. CLEMENTS, F. E., and GOLDSMITH, G. W. The phytometer method in ecology. Carnegie Inst. Wash. Publ. 356. 1924.
3. ————————, and LONG, FRANCES L. Factors in elongation and expansion under reduced light intensity. Plant Physiol. **9**: 767–781. 1934.
4. MARTIN, E. V. Effect of solar radiation on transpiration of *Helianthus annuus*. Plant Physiol. **10**: 341–354. 1935.
5. ————————, and CLEMENTS, F. E. Studies of the effect of artificial wind on growth and transpiration in *Helianthus annuus*. Plant Physiol. **10**: 613–636. 1935.
6. WEAVER, J. E., and CLEMENTS, F. E. Plant ecology. 1929.

Reprinted from PLANT PHYSIOLOGY, 9: 619–630, 1934.

EFFECT OF SOIL TEMPERATURE ON TRANSPIRATION IN *HELIANTHUS ANNUUS*

FREDERIC E. CLEMENTS AND EMMETT V. MARTIN

Introduction

In the researches upon the adaptation of transplants to alpine and dune habitats, it has been essential to develop field methods for analyzing the factor complex. Chief among these are control batteries of phytometers in which one major factor is maintained in a series of intensities or levels while the others are held practically uniform, except for the daily march. Water content, light, wind, and soil temperature in particular permit such manipulation, and all are under investigation in the series of transplant gardens at Pike's Peak and at Santa Barbara. In both the alpine climax and the xerosere of litoral dunes, instrumentation has shown that wind and soil temperature are relatively extreme, and much attention has in consequence been directed to them.

The first experiments in this field were conducted by WHITFIELD (**12, 13**) at the Alpine Laboratory in 1930–1931 by means of standardized phytometers of *Helianthus annuus,* and the native *Mertensia sibirica,* which is much utilized in the transplant project. He demonstrated that a reduction of soil temperature from 113° to 51° F. lowered transpiration very little, while a decrease from 51° to 34° F. exerted a pronounced influence. Records of soil temperature during the growing season at 12,000 feet in the alpine tundra of Pike's Peak indicated a range from 35° to 48° F., with an average of 44° F. for the four years of observation (**14**).

A physiological test indoors of the relation between temperature and absorption was long ago made by SACHS (**7**), who placed a well-watered tobacco plant in a warm room and surrounded the pot with ice. After a brief period the plant began to wilt, but when the ice was removed and the soil heated, it recovered without the addition of water. By means of potometers, VESQUE (**10**) found that within the limits of 10° to 15° C. the absorption by roots increased rapidly as the temperature rises. KOZAROW (**3**) employed the same method to show that a fall from 20° to 0° C. retarded the rate of water supply by 25–30 per cent. Later investigations by DELF (**2**), STILES and JØRGENSEN (**9**), and by WEBER and HOHENEGGER (**11**) agree in demonstrating that the rate of absorption by a plant cell always increases with a rise of temperature, at least up to 30° C. Such responses in absorption are naturally reflected in transpiration, although STAHL (**8**) has discovered that temperatures near 0° C. may still permit a slight loss of water.

Methods

For the earlier series, plants of *Helianthus annuus* were grown from seed in water-tight, cylindric, galvanized iron cans 8″ in diameter and 10″ in height, while for later ones similar cans $8\frac{1}{2}'' \times 11''$ were employed. Each of these was fitted with a removable lid that had in its center a circular opening 2″ in diameter. The soil used was a good loam of as nearly uniform texture and moisture as was feasible. The holard was set at approximately 65 per cent. of saturation (or 28 per cent. of the dry weight of the soil), and the total amount of water in each can was kept within 15 per cent. of this value throughout the growing period. When necessary, water was added through a glass tube extending into a layer of gravel about 1″ thick in the bottom of the can. When the plants were about six weeks old, the containers were sealed by adding a layer of sand about $\frac{1}{2}''$ thick on top of the soil, filling the opening in the lid with non-absorbent cotton, and corking the glass tube. The efficiency of this type of seal was tested by means of controls without plants. Weighings made on a torsion balance to the nearest gram during the time the experiments were in progress showed that such containers seldom lost a detectable amount. This seal has the advantage over the paraffin type in that forced aeration is unnecessary (Clements and Goldsmith, 1).

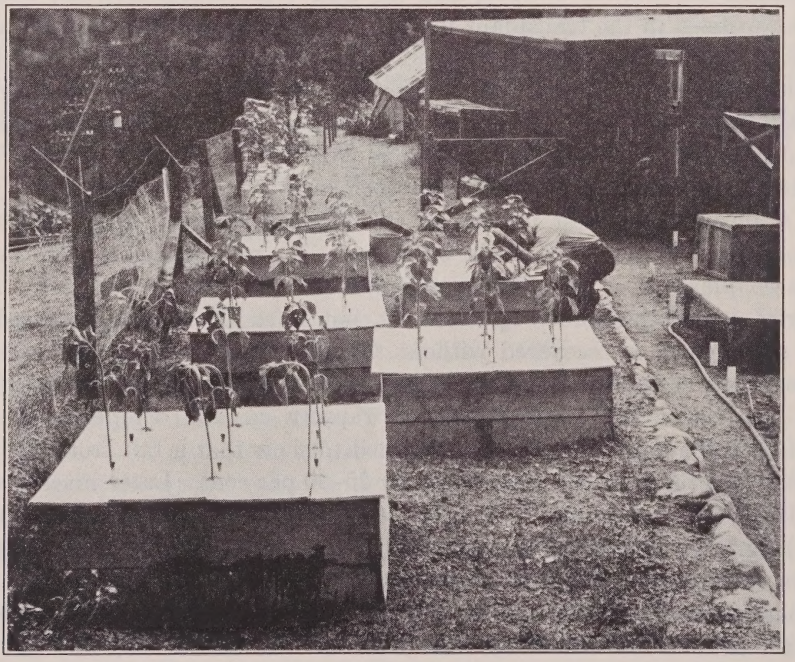

Fig. 1. Experimental installations as used in the later series, showing wilted condition of plants in a soil temperature of 34° F.

TABLE I

SOIL TEMPERATURE AND TRANSPIRATION

SERIES (1933)	AVERAGE SOIL TEMP.	INDIVIDUALS PER SET	TIME	TRANSPIRATION OF SET	SET LEAF AREA	TRANSPIRATION
	° *F.*		*hrs.*	*gm.*	*dm.*^{2}	*gm./dm.*^{2}*/hr.*
April 27	99	4	4.06	330	52.6	1.55
	73	.....	.....	295	53.1	1.37
	55	.....	.....	271	49.8	1.34
	46	.....	.....	254	54.5	1.15
	41	.....	.....	223	55.4	0.99
May 3	97	4	4.00	369	60.2	1.53
	74	.....	.....	339	51.5	1.65
	55	.....	.....	367	57.0	1.61
	47	.....	.....	318	53.9	1.47
	37	.....	.....	156	57.1	0.68
May 4	100	4	4.04	564	51.5	2.72
	75	.....	.....	485	60.2	1.99
	56	.....	.....	433	53.9	1.99
	48	.....	.....	348	57.1	1.51
	36	.....	.....	109	57.0	0.47
Aug. 25	99.5	9	4.31	379	60.3	1.46
	75	.....	.....	385	54.5	1.64
	55.5	.....	.....	374	58.0	1.50
	46	.....	.....	311	55.7	1.30
	36	.....	.....	143	58.8	0.56
Aug. 31	55.5	9	3.78	389	65.2	1.58
	51	.....	.....	382	62.9	1.61
	46	.....	.....	359	65.0	1.46
	40	.....	.....	272	69.0	1.04
	34	.....	.....	52	65.2	0.21
Sept. 2	52.5	9	4.09	835	68.3	2.98
	47	.....	.....	870	70.2	3.03
	42	.....	.....	752	72.3	2.54
	37.5	.....	.....	399	68.8	1.42
	34	.....	.....	138	68.8	0.49
Sept. 4	53	9	4.13	893	73.2	2.95
	47.5	.....	.....	910	72.5	3.04
	43	.....	.....	825	72.4	2.76
	38	.....	.....	562	69.6	1.81
	34.5	.....	.....	265	72.1	0.71

In the earlier series, five sets of four plants each were used, and these were placed in water baths 20″ square and 9″ deep, while in the later ones, five sets of nine plants each were employed with baths 3′ square and 10″ deep (fig. 1). In all cases these baths were held at fixed temperatures by additions of ice or hot water as occasion demanded, and any influence of the water on the immediate environment of the shoots was prevented by placing on the boxes closely fitting lids constructed of masonite or celotex.

On the day before a series was run, the phytometers were weighed and brought to their proper water content. At 6:00 A.M. the next day they were placed in the water baths, allowed four hours in which to become adjusted, and were then weighed to the nearest gram at 10:00 A.M. and again at 2:00 P.M. Soil temperatures were maintained constant throughout the series, and were registered by thermometers inserted near the centers of the cans. After the 2:00 P.M. weighing, the plants were taken out of the baths to permit recovery from any effects of the soil conditions, so as to be ready for future series. Leaf areas were determined in square decimeters by multiply-

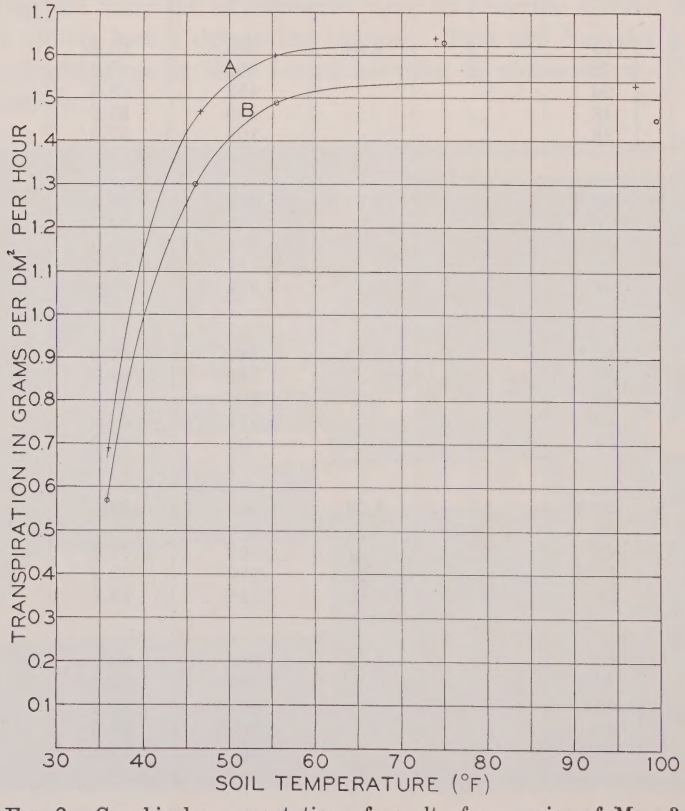

FIG. 2. Graphical representation of results from series of May 3 (A) and August 25 (B).

ing the product of length and width of the leaves in centimeters by the factor 0.013, according to the method of CLEMENTS and GOLDSMITH (1).

Results

In table I are given the data taken on seven different days, and in figure 2 the results for May 3 and August 25, 1933, are represented graphically

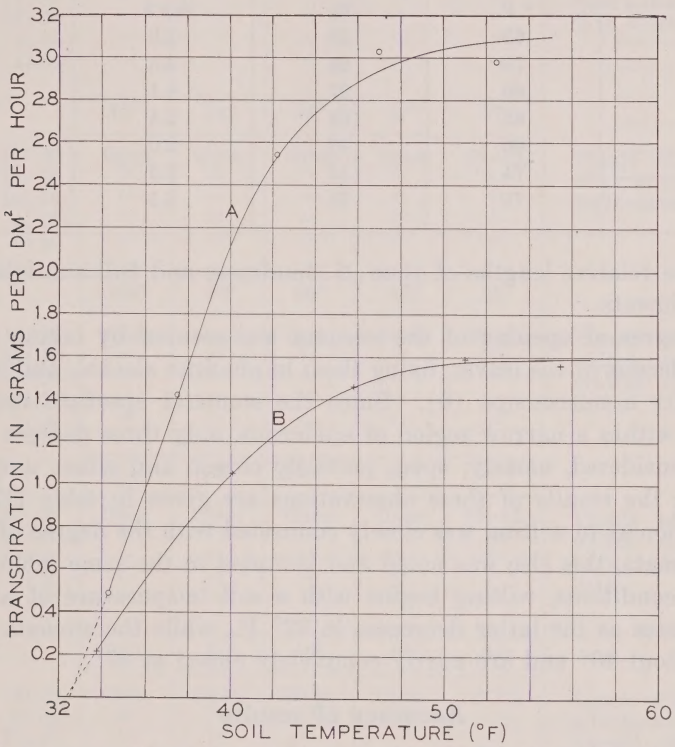

FIG. 3. Graphical representation of results from series of September 2 (A) and August 31 (B).

by curves A and B respectively, which portray transpiration in grams per square decimeter per hour (ordinate) as a function of soil temperature in degrees Fahrenheit (abscissa). Similarly, the data for September 2 and August 31, 1933, are represented in figure 3 by curves A and B respectively. The differences between the results for different days are due partly to the fact that the plants vary in age and partly to diversity in environmental factors (table II). Air temperature and relative humidity were measured at regular intervals during the various series, while the average wind velocity was obtained from the readings of a Weather Bureau four-cup anemometer. The light intensity was obtained from an estima-

TABLE II

METEOROLOGICAL DATA

DATE	AVERAGE AIR TEMPERATURE	AVERAGE RELATIVE HUMIDITY	AVERAGE WIND VELOCITY	LIGHT, ESTIMATED % FULL SUNLIGHT
	° *F.*	%	*m.p.h.*	%
April 27	65	49	1.9	25
May 3	73	24	3.5	100
May 4	80	27	4.1	100
Aug. 25	65	53	2.4	75
Aug. 31	66	45	2.0	50
Sept. 2	74	12	2.5	100
Sept. 4	75	21	2.1	100

tion of the relative lengths of time of cloudiness and full sunlight during the experiments.

The degree of opening of the stomata was secured by taking strips of lower epidermis of the leaves, fixing them in absolute alcohol, and observing them under a microscope (**6**). Since the stomatal aperture varied considerably within a narrow region of epidermis, only three degrees of opening are considered, namely, open, partially closed, and either narrow slits or closed; the results of these observations are given in table III. Since the condition as to wilting was closely connected with the degree of opening of the stomata, this also was noted and included in the same table. Under ordinary conditions, wilting begins with a soil temperature of about 40° and increases as the latter decreases to 32° F., while the stomata begin to close at about 40° and are nearly completely closed at 37°.

Accuracy of results

Errors in this type of experiment arise mainly from two sources, the experimental method and the differences between individual plants. The latter are caused principally by variations in growth or structure and differences in shading of lower leaves by the upper ones, while the former includes errors in the phytometer method, in leaf measurements, and in the weighing itself, as well as those arising from the length of time required to weigh the entire group of plants, which in these series amounted to about 25 minutes.

In order to discover the approximate values of the errors due to these various causes, 52 phytometers of *Helianthus annuus* were grown under similar conditions, both of soil and atmosphere, up to seven weeks of age. These were sealed as described and weighed at 10:00 A.M. and 2:00 P.M. on each of three successive days. The water content was maintained ap-

TABLE III

STOMATAL OPENING AND WILTING

DATE	TIME	AVERAGE SOIL TEMPERATURE					REMARKS ON WILTING
		99°	73°	55°	46°	41°	
April 27	10:00	Open	Open	Open	Open	P. Cl.*	Leaves of plants at 41° were a little less turgid than normally
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	
		97°	74°	55°	47°	37°	
May 3	10:00	Open	Open	Open	Open	Sl.–Cl.	Plants at 37° somewhat wilted; edges of leaves curled a little
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	
		100°	75°	56°	48°	36°	
May 4	10:00	Open	Open	Open	Open	Sl.–Cl.	Plants at 36° were wilted so that the crowns bent over a little
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	
		99.5°	75°	55.5°	46°	36°	
Aug. 25	10:00	Open	Open	Open	Open	Sl.–Cl.	Plants at 36° were wilted so that the crowns bent over a little
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	
		55.5°	51°	46°	40°	34°	
Aug. 31	8:00	Open	Open	Open	Open	P. Cl.	Leaves of plants at 40° a little less turgid than normal; plants at 34° wilted so that crowns bent over considerably
	9:00	"	"	"	"	"	
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	
		52.5°	47°	42°	37.5°	34°	
Sept. 2		Strips unsatisfactory					Leaves of plants at 37.5° drooped and curled a little; plants at 34° wilted so that the crowns bent at nearly right angles to the main stem (fig. 1)

TABLE III—(*Continued*)

STOMATAL OPENING AND WILTING

DATE	TIME	AVERAGE SOIL TEMPERATURE					REMARKS ON WILTING
		53°	47.5°	43°	38°	34.5°	
Sept. 4	8:00	Open	Open	Open	Open	Open	Leaves of plants at 38° drooped and curled a little; plants at 34.5° wilted considerably, but crowns did not bend over
	9:00	"	"	"	"	P. Cl.	
	10:00	"	"	"	P. Cl.	Sl.–Cl.	
	11:00	"	"	"	"	"	
	12:00	"	"	"	"	"	
	1:00	"	"	"	"	"	
	2:00	"	"	"	"	"	

* P. Cl., partially closed; Sl.–Cl., openings are either slits or are closed. Measurements of the stomatal openings for the earlier series were made by DR. F. L. LONG of the Carnegie Institution of Washington.

proximately constant by adding the proper amount each day. Leaf areas were measured on the first and third days, and the averages of these two were taken as the values for the intermediate day.

The average transpiration in grams per square decimeter per hour for the 4-hour period and the deviations of the individuals from this value were calculated. Since it required 30 minutes to weigh the 52 phytometers, the transpiration of the first plant weighed was measured for the period 10:00–2:00, while that of the last plant was from 10:30–2:30, the others falling between these two extremes. Since no drift in the deviations of the individuals was discernible, it was concluded that any error caused by lack of simultaneity of weighing was within the limits imposed by other sources. An approximate value of the error introduced by the latter was obtained in the following manner from the deviations of the individuals. The 52 phytometers were divided at random into 13 sets of four each, and the average transpiration for each set was determined for each of the three days. The maximum deviation of any one set from the average of the 13 sets for each day was 9 per cent., while the average deviation was 3 per cent. Similarly, when the 52 plants were grouped into sets of nine each, the maximum deviation observed was 4 per cent. and the average 1.5 per cent. It is probable, however, that the data obtained with the soil temperature experiments are not altogether as accurate as these figures indicate, since a slight error may arise from the effect of the water baths on the air about the plants, especially when the lids are lifted. In the measurement of temperature there may be appreciable errors due partially to gradients within the baths and partly to fluctuations about the average. Such deviations can only be estimated, but it is probable that the averages given in table I are in error by not more than about 1° F.

Discussion

In representing the data by smoothed curves as in figures 2 and 3, it is assumed that the relation between soil temperature and transpiration is a continuous one, and this assumption seems to be justified by the accuracy with which the curves fit the points. As can be seen from the curves, transpiration varies very little with soil temperatures between 55° and 100° F., but falls off below about 55° and is reduced to half at about 38°. Extrapolation of the curves in figure 3 indicates that transpiration approaches zero at 32.5°, although the accuracy of the data is not sufficient to fix this point at 32.5° and not 32° as is to be expected.

Obviously the explanation of this reduction in transpiration with soil temperatures below 55° F. is that the absorbing capacity of the root system is lowered, thus reducing the water supplied to the leaves. This usually does not produce a noticeable loss of turgor until the temperature has been decreased to about 40° F. The degree of wilting increases as the temperature is reduced below 40°, and at 34° has proceeded so far that the crowns of the plants are bent at nearly right angles to the main stems (table III). This wilting did not continue long enough to cause the plants any permanent injury, as was shown by the following test: On August 25, 1933, the set of plants at 36° F. (table I) was removed from its bath at 2:50 P.M. and placed in the 75° bath. This set and the one at 55.5° were weighed again at 4:00 P.M. and at 5:00 P.M. During the period from 2:50 to 4:00 the losses were 1.02 and 1.55 gm./dm.^{2}/hr. respectively, while during that from 4:00 to 5:00 the losses were 0.48 and 0.51 gm./dm.^{2}/hr. respectively. For this latter period the set that had wilted lost practically as much water as the set that had not. Also, by 4:00 P.M. the soil temperatures of both sets were about 55°, and none of the plants gave any visual signs of having been wilted.

The condition of the stomata during the various series is indicated in table III. Only three degrees of opening are considered, open, partially closed, and either narrow slits or closed, denoted in the table by the symbols Open, P.Cl., and Sl.–Cl., respectively. The stomata did not start to close until the soil temperature had been lowered to the point where the plants began to wilt perceptibly, about 40° F., but they were almost completely closed at 37°. These results indicate that it is not necessary for the stomata to close in order for transpiration to be reduced. For example, at 45° F. the transpiration was lowered appreciably, but the stomata showed no signs of closing; hence, the reduced water loss in this case must be due to a reduction in the water supplied to the leaves, which is in turn caused by a decrease in the absorbing capacity of the root system. Whether the amount of water transpired represents the amount absorbed during the same period of time is questionable, but since the degree of wilting of the

plants appeared to remain constant throughout the weighing period, it seems probable that such is the case.

KRAMER (**4**) points out that absorption of water by roots may be affected by temperature in two ways: first, by the physical effects (largely increased viscosity and decreased vapor pressure) which result in a slower movement of water from soil to root; and second, by the physiological effects on the permeability of the root cells. He gives data showing that the absorption of water from loam by soil-points (LIVINGSTON and KOKETSU, **5**) at 60° F. is approximately twice that at 32° F. Whether these results can be considered as a measure of the physical effects of low soil temperature on absorption of water by roots is questionable; but if so, then the results obtained with phytometers of *Helianthus annuus* indicate that the physiological effects are of greater importance than the physical.

The data presented here agree with those of the earlier workers already mentioned, and they also constitute an addition to present knowledge in that the effect upon transpiration of soil temperature has been traced through the critical region 34° to 55° F. So far as is known, this range has not heretofore been investigated.

The applicability of these results to alpine problems is definitely limited in that the plants were grown under soil temperatures of 60°–70° F., and the effect of lower soil temperatures upon transpiration has been measured for only the first few hours after the plants were subjected to those conditions. However, since WHITFIELD (**12**) has shown that transpiration of phytometers of *Helianthus annuus* in alpine regions (12,000 feet on Pike's Peak) may be as much as 2 gm./dm^2./hr., the results of curve B of figure 3 are applicable to this climatic region. Soil temperatures in this same climate are represented graphically in figure 4 (taken from WHITFIELD, **14**),

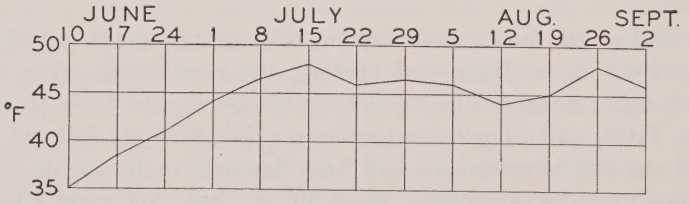

FIG. 4. Average soil temperature at 4 inches, by weeks 1927–1930, at 12,000 feet on Pike's Peak (from WHITFIELD, 1933).

which shows that there is a variation between 35° and 48° F. for the growing season. Accordingly our results indicate that, in this particular alpine climate at least, soil temperature probably has an appreciable influence on transpiration and growth of vegetation. These results are obtained with phytometers of *Helianthus annuus,* however, and it is possible that native alpine plants would respond differently.

The final test of this influence remains to be carried out. Experiments are planned in which plants will be grown in the field from seeds or seedlings under various soil temperatures with other environmental factors similar, and the growth, transpiration, and other functional activities will be measured. This problem will require several thermostatically controlled baths, but it is expected to yield considerable information concerning the effect of low soil temperature on vegetation.

Summary

1. The effect of soil temperatures in the range 34°–100° F. on transpiration of *Helianthus annuus* phytometers 6–8 weeks old was measured by using five sets of four or nine plants each, run simultaneously in water baths of different temperatures.

2. It was found that transpiration varies very little with soil temperatures between 55° and 100°, but drops rapidly below 55°, was reduced to half at 38°, and approached zero at 32°.

3. The temperature of the baths was held constant within 1° F., and some data are presented that indicate an accuracy in transpiration measurements of from 3 to 5 per cent.

4. Strips of lower epidermis of the leaves show that the stomata do not begin to close until the soil temperature is lowered to about 40°, but are nearly completely closed at 37° F.

5. The plants usually start to wilt at about 40° and at 34° are wilted so that the crowns are bent at nearly right angles to the main stems.

6. The plants recover rapidly from the wilted condition when the soil temperature is raised.

Carnegie Institution of Washington
Santa Barbara, California

LITERATURE CITED

1. Clements, F. E., and Goldsmith, G. W. The phytometer method in ecology. Carnegie Inst. Washington Publ. No. 356. 1924.
2. Delf, M. Studies of protoplasmic permeability by measurement of rate of shrinkage of turgid tissues. I. The influence of temperature on the permeability of protoplasm to water. Ann. Bot. **30**: 283–310. 1916.
3. Kozarow, P. Einfluss verschiedener äusserer Faktoren auf die Wasseraufnahme der Pflanzen. Dissert., Leipzig. 1897.
4. Kramer, P. J. Effects of soil temperature on the absorption of water by plants. Science **79**: 371–372. 1934.
5. Livingston, B. E., and Koketsu, R. The water-supplying power of

the soil as related to the wilting of plants. Soil Sci. **9**: 469–485. 1920.

6. Lloyd, F. E. The physiology of stomata. Carnegie Inst. Washington Publ. No. 82. 1908.
7. Sachs, J. Beiträge zur Lehre von der Transpiration der Gewächse. Bot. Zeit. **18**: 121–126. 1860.
8. Stahl, E. Zur Physiologie und Biologie der Exkrete. Flora **113**: 1–132. 1919.
9. Stiles, W., and Jörgensen, I. Studies in permeability. V. The swelling of plant tissues in water and its relation to temperature and various dissolved substances. Ann. Bot. **31**: 415–434. 1917.
10. Vesque, J. De l'influence de la température du sol sur l'absorption de l'eau par les racines. Ann. Sci. Nat. Bot. **6**: 169–209. 1878.
11. Weber, F., and Hohenegger, H. Reversible Viscositätserhöhung des Protoplasmas durch Kälte. Ber. deut. bot. Ges. **41**: 198–205. 1923.
12. Whitfield, C. J. Ecological aspects of transpiration. I. Pike's Peak region; climatic aspects. Bot. Gaz. **93**: 436–452. 1932.
13. ————. Ecological aspects of transpiration. II. Pike's Peak and Santa Barbara regions; climatic and edaphic aspects. Bot. Gaz. **94**: 183–196. 1932.
14. ————. The vegetation of the Pike's Peak region. Ecol. Mon. **3**: 75–105. 1933.

Reprinted from PLANT PHYSIOLOGY, 10: 613–636, 1935.

STUDIES OF THE EFFECT OF ARTIFICIAL WIND ON GROWTH AND TRANSPIRATION IN *HELIANTHUS ANNUUS*

EMMETT V. MARTIN AND FREDERIC E. CLEMENTS

Introduction

Although considerable attention has been given to the influence of wind on transpiration, the results that have been obtained are very conflicting. Practically all control experiments with this factor have been in the region of very low velocities. KNIGHT (**12**) found that a wind velocity of 7 meters per minute (0.26 miles per hour) caused an increase in the rate of transpiration of about 50 per cent. STÅLFELT (**21**), using single detached leaves suspended in an analytical balance case, obtained a very rapid rise with wind up to a velocity of 10 meters per minute, a slower increase from there to 30 m./min., but no further increase as the wind rose to 60 m./min. (2.24 miles per hour). This maximum increase was 140 per cent. of the value with no wind. FIRBAS (**8**), who employed cut shoots under a wind velocity of 3.75 m./sec., obtained similar results with low rates of transpiration, but with high rates (shoots in direct sunlight) wind actually caused a decrease. SEYBOLD (**18, 19, 20**) concluded that wind has no influence on stomatal transpiration but only on the cuticular component, the result being that only those plants with a high cuticular transpiration, namely hydrophytes, showed an appreciable increase in the transpiration rate due to the action of wind.

Observations on water losses of plants under natural conditions have also yielded conflicting results. COPELAND (**6**) found an increase in the transpiration rate of cocoanut palm in full sunlight of about 100 per cent. with a wind velocity estimated at 5 miles per hour. Others (**4, 9**) have noted an increase with velocities up to 8 miles per hour, but a retardation with higher velocities. WILSON (**22**) observed that the rate of transpiration of some Australian plants was checked when the wind velocity rose to 20 miles per hour. BRIGGS and SHANTZ (**2, 3**), however, concluded from their studies of the correlation between environmental factors and transpiration rates for the growing season that only from 2 to 6 per cent. of the water loss could be attributed directly to the action of wind.

Nearly all the control work in this field has been with cut shoots or leaves, which rarely give dependable results, while that with rooted plants has for the most part been under natural conditions with no attempt to control the wind velocity. A combination of these methods has been utilized

in the present work by growing plants in cans but under otherwise natural conditions and producing artificial wind by means of large fans.

These fans have also been employed in a study of the effect of continuous wind upon plant growth. Although the depressing effect of wind has long been recognized, very few measurements of a quantitative nature have been made. BLANCHARD (1) compared the growth and yield of two orchards of Eureka lemons and found that the factor of improvement in yield due to protection from wind was 5 to 7 and in size of trees about 3. FINNELL (7) has grown marigolds under a constant wind velocity of 15 miles per hour and found that it caused a reduction of about 50 per cent. in dry weight of material produced.

I. Effect of wind on transpiration; short time series

METHODS

For all series, plants of *Helianthus annuus* were grown from seed in water tight, cylindric, galvanized iron cans 8 in. in diameter and 10 in. in height. Each of these was fitted with a removable lid that had in its center a circular opening 2 in. in diameter. The soil used was a good loam of as nearly uniform texture and moisture as was feasible. The holard was set at approximately 65 per cent. of saturation (or 28 per cent. of the dry weight of the soil), and the total amount of water in each can was kept within a few per cent. of this value throughout the growing period as well as during the test series. When necessary, water was added through a glass tube extending into a layer of gravel about 1 in. thick in the bottom of the can. When the plants were 6 to 8 weeks old, the containers were sealed by adding a layer of sand about $\frac{3}{4}$ in. thick on top of the soil, filling the opening in the lid with non-absorbent cotton, and corking the glass tube. The efficiency of this seal was tested by means of controls without plants. Weighings made on a torsion balance to the nearest gram during the time the experiments were in progress showed that these containers seldom lost a detectable amount.

Wind was produced by fans taken from Pierce-Arrow and Packard motor cars, mounted on specially constructed supports, and driven by $\frac{1}{3}$ h.p. induction motors. The wind velocity was regulated partly by pulley ratio and partly by adjusting the distance of the fans from the plants. Velocities from about 0.5 to 25 miles per hour were obtainable with this installation and measurements were made by means of a small fan type anemometer.

In all series, two sets of four plants each were used, one serving as a test set, the other as a control. The two sets were selected from a large group in order that they might be as nearly alike as possible. To obtain conditions sufficiently calm for these experiments, it was necessary to work inside the greenhouse, since there is practically always some movement of

TABLE I

TRANSPIRATION RATES IN GRAMS PER SQUARE DECIMETER PER HOUR FROM SERIES TAKEN INSIDE GREENHOUSE

DATE		NO WIND		WIND = 0.8 M.P.H.					NO WIND		WIND
5/8/35	Time interval	9:30–10:30	10:30–11:30	11:30–12:00	12:00–12:30	12:30–1:30	1:30–2:30	2:30–3:30	3:30–5:00	5:00–8:00	8:00 P.M. 8:30 A.M.
	T_a*	0.512	0.539	0.678	0.892	1.08	1.10	1.33	0.787	0.308	0.152
	T_b	0.499	0.544	0.859	1.23	1.38	1.47	1.81	0.727	0.272	0.189
	T_b/T_a	0.98	1.01	1.25	1.38	1.28	1.34	1.36	0.92	0.88	1.24
		NO WIND		WIND = 2.1 M.P.H.					NO WIND		WIND
5/9/35	Time interval	8:30–9:30	9:30–11:30	11:30–12:00	12:00–12:30	12:30–1:30	1:30–2:30	2:30–3:30	3:30–5:00	5:00–9:30	9:30 P.M. 8:30 A.M.
	T_a*	0.535	0.605	0.757	0.854	0.850	0.542	0.516	0.445	0.160	0.108
	T_b	0.578	0.593	1.05	1.25	1.16	0.637	0.711	0.548	0.146	0.136
	T_b/T_a	1.08	0.98	1.39	1.46	1.37	1.18	1.38	1.23	0.91	1.26
		NO WIND		WIND = 5.5 M.P.H.					NO WIND		WIND
5/10/35	Time interval	8:30–10:15	10:15–11:30	11:30–12:00	12:00–12:30	12:30–1:30	1:30–2:30	2:30–3:30	3:30–5:15	5:15–8:30	8:30 P.M. 8:00 A.M.
	T_a*	0.344	0.707	0.972	1.20	0.682	0.717	1.09	0.595	0.213	0.127
	T_b	0.340	0.710	1.57	1.59	0.865	1.01	1.50	0.540	0.195	0.159
	T_b/T_a	0.99	1.00	1.61	1.32	1.27	1.41	1.38	0.91	0.91	1.25
		NO WIND		WIND = 9.5 M.P.H.					NO WIND		WIND
5/11/35	Time interval	8:00–9:40	9:40–11:40	11:40–12:00	12:00–12:30	12:30–1:30	1:30–2:30	2:30–3:30	3:30–5:30	5:30–8:30	8:30 P.M. 7:30 A.M.
	T_a*	0.590	1.52	2.24	2.29	2.63	2.34	1.64	0.676	0.161	0.122
	T_b	0.572	1.57	4.44	3.21	3.98	3.16	2.25	0.568	0.136	0.179
	T_b/T_a	0.97	1.03	1.98	1.40	1.51	1.35	1.37	0.84	0.84	1.47

* T_a and T_b are the transpiration rates of the two sets of plants *a* and *b*, while their ratio is given by T_b/T_a. Set *a* is the control and has no wind at any time, while *b* is the test set and has wind during the periods indicated.

TABLE I—(*Continued*)

TRANSPIRATION RATES IN GRAMS PER SQUARE DECIMETER

DATE		NO WIND			WIND = 16 M.P.H.				
	Time interval	8:30–9:30	9:30–10:30	10:30–11:50	11:50–12:05	12:05–12:30	12:30–2:00	2:00–2:30	2:30–3:30
5/14/35	T_a*	1.05	0.95	1.16	1.18	0.99	1.11	0.86	0.75
	T_b	1.01	1.07	1.07	2.81	1.23	1.53	1.29	1.18
	T_b/T_a	0.96	1.13	0.92	2.38	1.24	1.38	1.50	1.57
		NO WIND		WIND = 2.6 M.P.H.			NO WIND		
	Time interval	9:30–10:10	10:10–10:48	10:48–11:03	11:03–11:38	11:38–12:41	12:41–1:34	1:34–2:38	
5/15/35	T_a	0.99	0.95	0.79	0.80	0.69	0.79	1.22	
	T_b	1.05	0.89	1.41	0.96	0.91	0.71	1.19	
	T_b/T_a	1.06	0.94	1.78	1.20	1.32	0.90	0.97	
		NO WIND	WIND = 0.7 M.P.H.			NO WIND			
	Time interval	8:00–9:44	9:44–9:59	9:59–10:37	10:37–11:34	11:34–11:49	11:49–1:13	1:13–4:59	4:59–5:45
5/16/35	T_a	1.15	1.97	2.08	2.49	2.89	2.85	2.13	1.10
	T_b	1.20	2.44	2.44	3.16	2.66	2.66	2.06	1.28
	T_b/T_a	1.04	1.24	1.17	1.27	0.92	0.93	0.97	1.16

* T_a and T_b are the transpiration rates of the two sets of plants *a* and *b*, while their ratio is wind during the periods indicated.

air in the open. The greenhouse measures 39 ft. × 16 ft., and hence is quite large enough for the purpose. Stomatal openings were determined at regular and frequent intervals during each series by means of the well known alcohol method (LLOYD, **14**). Leaf areas in square decimeters were determined by multiplying the product of the length and width of each leaf in centimeters by the factor 0.0134 (CLEMENTS and GOLDSMITH, **5**).

RESULTS

The transpiration measurements from seven representative series are given in table I, in which T_a denotes the rate of transpiration of the control set of plants in grams per square decimeter per hour, T_b that of the test set, and T_b/T_a the ratio of the rate of water loss of *b* to that of *a*. These results are shown graphically in figures 1 and 2, which portray the transpiration rate of the test set in percentage of that of the control. Each series began in the morning with one or more periods during which neither set had any wind, followed by several hours of wind, a second check period of two, and

TABLE I—(*Continued*)

PER HOUR FROM SERIES TAKEN INSIDE GREENHOUSE

No wind		Wind	No wind				
3:30–6:00	6:00–8:45	8:45 P.M. 8:50 A.M.	8:50 A.M. 10:15 A.M.				
0.524	0.133	0.151	0.95				
0.510	0.177	0.302	0.94				
0.97	1.33	2.00	0.99				

Wind = 5.4 m.p.h.				No wind			
2:38–2:53	2:53–3:23	3:23–3:53	3:53–5:18	5:18–5:33	5:33 P.M. 8:00 A.M.		
1.13	1.23	0.92	0.91	0.70	0.170		
2.14	1.55	1.05	1.32	0.59	0.166		
1.89	1.26	1.14	1.45	0.84	0.98		

Wind = 16 m.p.h.					No wind		
5:45–6:00	6:00–6:15	6:15–6:30	6:30–8:15	8:15 P.M. 8:28 A.M.	8:28–8:44	8:44–9:03	9:03–10:06
1.04	0.70	0.475	0.219	0.250	1.44	1.54	1.96
2.08	0.92	0.703	0.386	0.384	1.10	1.44	1.75
2.00	1.31	1.48	1.76	1.54	0.76	0.93	0.89

given by T_b/T_a. Set *a* is the control and has no wind at any time, while *b* is the test set and has

finally usually wind again during the night. For all series, the losses of the two sets during the initial check periods were the same within a few per cent., but when the wind was turned on the test set, its transpiration rate invariably rose with respect to that of the control, the increase depending on the wind velocity.

For the low velocity winds, up to about 2 miles per hour, the transpiration rate increased from 20 to 30 per cent., and this value was maintained approximately constant during the entire time the wind was turned on. For higher velocities, however, there was a comparatively high initial rise lasting no more than 15 minutes and in many cases probably less, followed by a much lower value, after which there was usually a gradual increase. This high initial rise increased with rising wind velocity, being 78 per cent. for 2.6 m.p.h., 89 for 5.4, 98 for 9.5, and 138 for 16 m.p.h. These values are considerably higher than the averages for the entire periods that the wind was acting. These latter values are given in table II, for both the day and night periods, and the daytime ones are shown graphically in figure 3. The

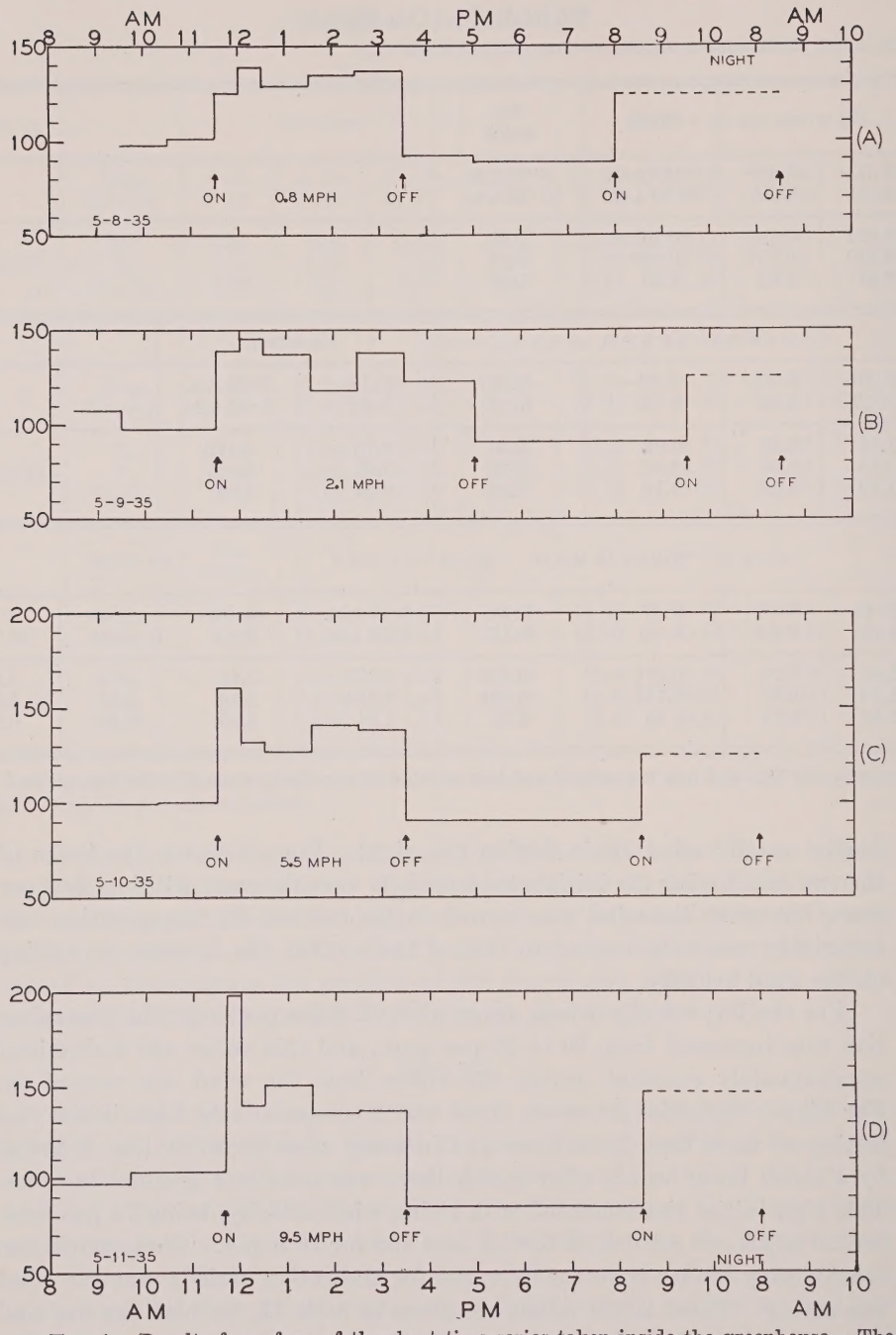

FIG. 1. Results from four of the short time series taken inside the greenhouse. The ordinate represents the transpiration rate of the test set in percentage of that of the control, while the abscissa indicates time of day. Values obtained during the night are shown by the dashed lines.

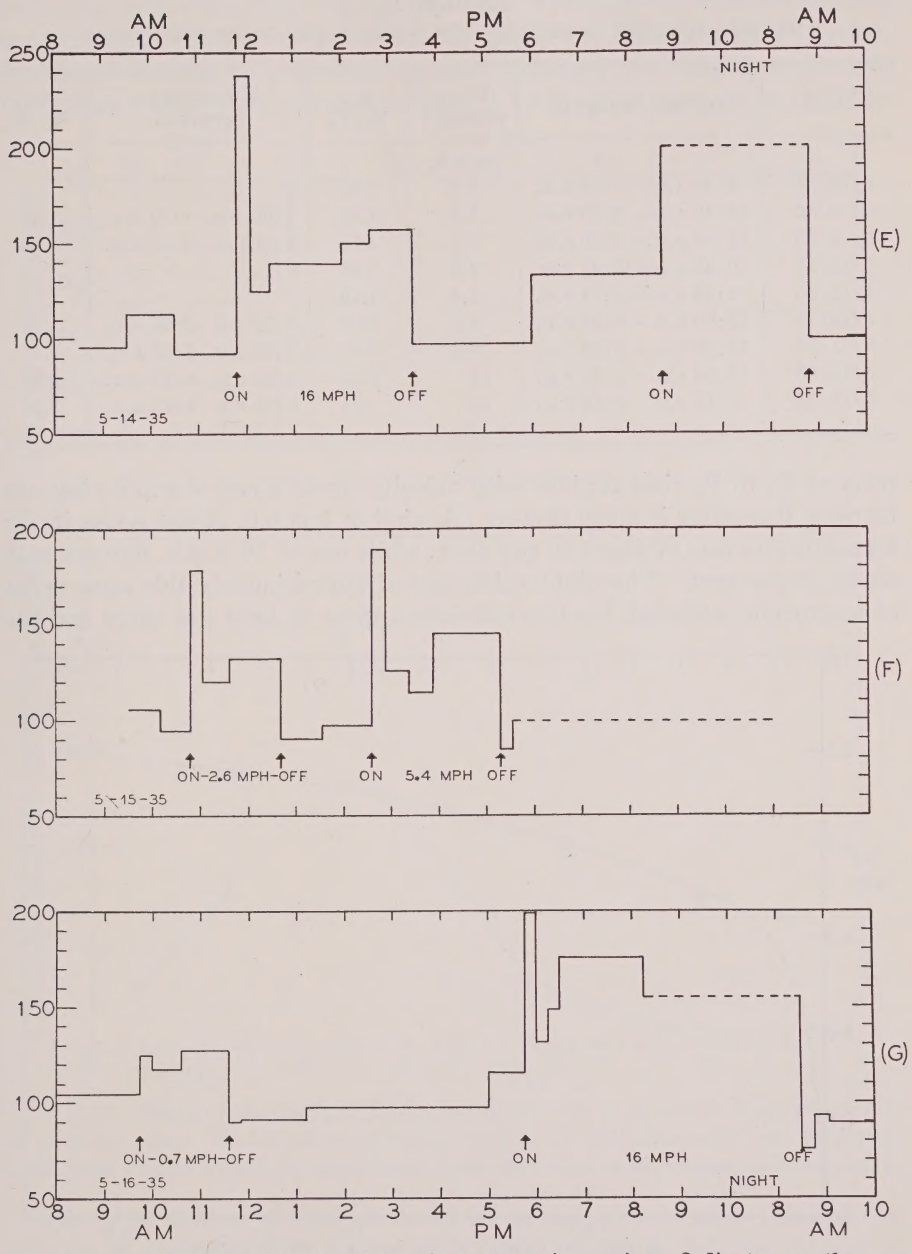

FIG. 2. Results from three others of the short time series. Ordinates are the same as in figure 1.

TABLE II

GENERAL SUMMARY OF RESULTS FROM SERIES TAKEN INSIDE GREENHOUSE

DATE	DAYTIME INTERVAL	WIND VELOCITY	AV. T_b/T_a	NIGHTTIME INTERVAL	AV. T_b/T_a
		m.p.h.			
5/16/35	9:44 A.M.–11:34 A.M.	0.7	1.23	.....	.....
5/ 8/35	11:30 A.M.– 3:30 P.M.	0.8	1.32	8:00 P.M.–8:30 A.M.	1.24
5/ 9/35	11:30 A.M.– 5:00 P.M.	2.1	1.34	9:30 P.M.–8:50 A.M.	1.26
5/15/35	10:48 A.M.–12:41 P.M.	2.6	1.34	.....	.....
5/15/35	2:38 P.M.– 5:18 P.M.	5.4	1.40	.....	.....
5/10/35	11:30 A.M.– 3:30 P.M.	5.5	1.38	8:30 P.M.–8:00 A.M.	1.25
5/11/35	11:40 A.M.– 3:30 P.M.	9.6	1.46	8:30 P.M.–7:30 A.M.	1.47
5/14/35	11:50 A.M.– 3:30 P.M.	16	1.50	8:45 P.M.–8:50 A.M.	2.00
5/16/35	5:45 P.M.– 8:15 P.M.	16	1.71	8:15 P.M.–8:28 A.M.	1.54

ratio of T_b to T_a rises rapidly with velocity up to about 2 m.p.h., but the increase thereafter is much slower. A wind of 1 m.p.h. causes a rise in the transpiration rate of about 30 per cent., while one of 16 m.p.h. induces only about 50 per cent. The night values are of approximately this same order of magnitude, although the low velocities appear to have less effect and the

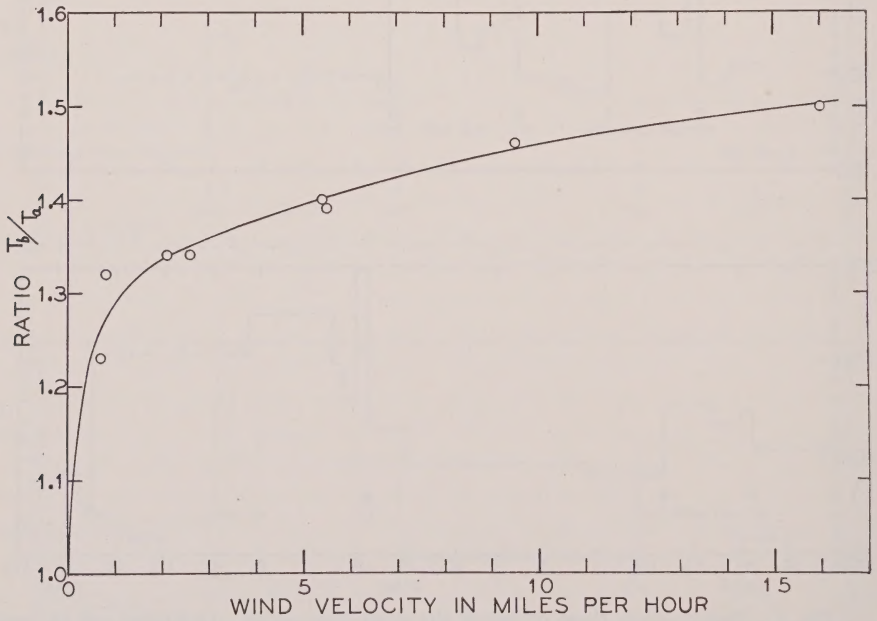

FIG. 3. The ratio of the transpiration rate of the test set (T_b) to that of the control (T_a) represented as a function of wind velocity. The values are all averages for from 2 to 4 hours of wind during the daytime hours.

high ones more effect than during the day. Although the *relative* increase in transpiration rate during the night is nearly the same as during the day, the *actual* increase in grams per square decimeter per hour is much less. This effect is shown graphically in figure 4 by the data taken May 11, 1935.

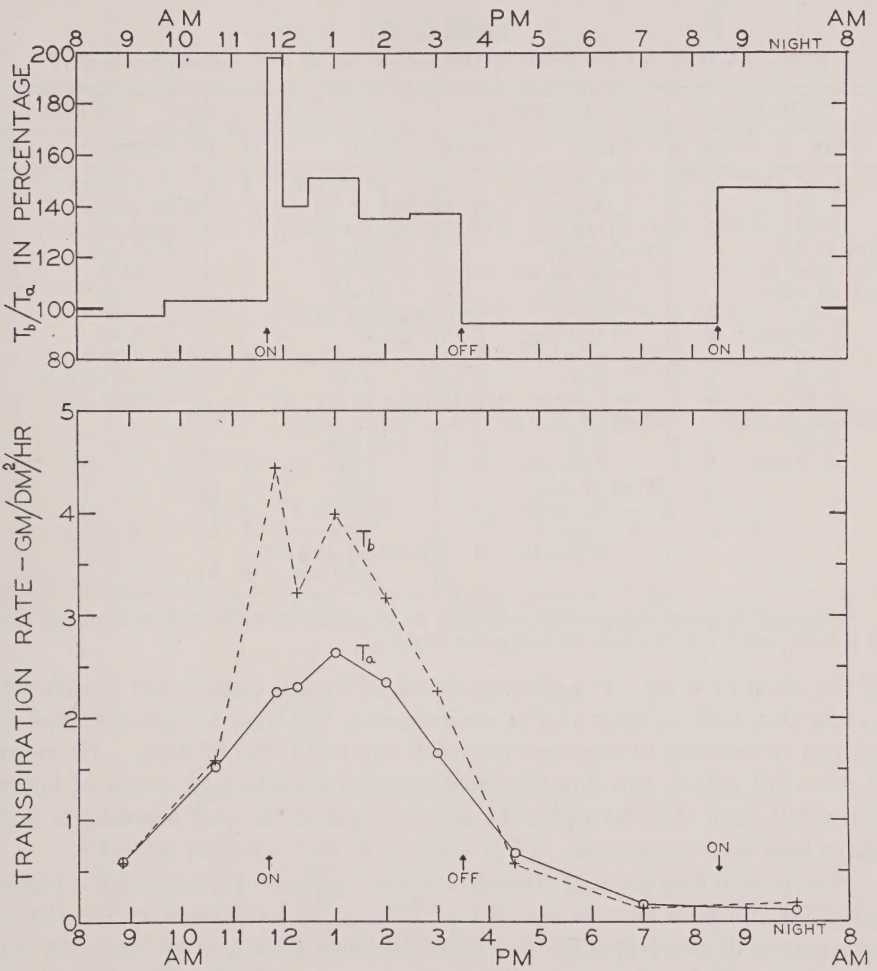

FIG. 4. Results from the short time series of May 11, 1935, with a wind velocity of 9.5 miles per hour. The actual transpiration rates of the test and control sets are shown in the lower part as T_b and T_a respectively, while their ratio in percentage is shown above.

The lower section of figure 4 shows the actual transpiration rates of the two sets of plants and the upper their ratio. Wind in this case caused a rise of about 46 per cent. both day and night, although the actual increase in grams per square decimeter per hour during the day was about 20 times as great as during the night.

The behavior of the stomata during the various series depended on the wind velocity, currents below about 2 m.p.h. having no observable effect, those above this value usually showing a distinct influence. The stomatal openings for some of the series, given in table III, show the action typical

TABLE III

STOMATAL OPENINGS FOR SOME OF THE SERIES TAKEN INSIDE THE GREENHOUSE

5/10/35			5/11/35			5/15/35			5/16/35		
TIME	*a*	*b*	TIME	*a*	*b*	TIME	*a*	*b*	TIME	*a*	*b*
8:30 A.M.	5	5	8:00 A.M.	5	5	10:50 A.M.	5	5	5:45 P.M.	3	3
10:30	5	5	9:45	5	5	Wind of 2.6			Wind of 16		
11:30	5	5	11:30	5	5	m.p.h on at			m.p.h. on at		
Wind of 5.5			Wind of 9.5			10:50 A.M.			5:45 P.M.		
m.p.h on at			m.p.h. on at			11:10	5	1	6:00	3	1
11:30 A.M.			11:40 A.M.			11:45	5	2	6:15	3	1
12:00	5	1	12:00	5	0	Wind off at			6:30	3	1
12:30 P.M.	5	1	12:30 P.M.	5	1	12:42			8:20	0	0
1:30	4	1	1:30	5	1	12:45 P.M.	5	2	8:30 A.M.	5	3
2:30	4	1	2:30	5	1	2:35	5	4	Wind off at 8:30		
3:30	4	1	3:30	5	1	Wind of 5.4			10:15 A.M.	5	5
Wind off at 3:30			Wind off at 3:30			m.p.h. on at					
5:15	1	3	5:30	2	1	2:38 P.M.					
8:15 P.M.	0	1	8:30 P.M.	0	0	3:00	5	1			
			Wind of 9.5			3:30	5	1			
			m.p.h. on at			4:00	4	1			
			8:30 P.M.			5:20	3	2			
			7:30 A.M.	4	2	Wind off at 5:20					
						8:00 A.M.	5	5			

*Stomatal openings are graded according to an arbitrary scale with 0 denoting closed and 5 wide open; *b* is the test set and *a* the control.

of the effect of wind. The stomata closed, although usually not completely, in less than half an hour and in some cases in less than 15 minutes, and remained so the rest of the day, provided the wind was blowing. However, if the wind ceased, the stomata usually reopened within a couple of hours. When the wind blew all night, the stomata opened the next morning to only about half their maximum. (For other pertinent data see table IV.)

The high initial rates of transpiration at the onset of wind of the higher velocities caused a certain amount of wilting, as evidenced by the flaccid appearance of the leaves at the end of the first period after the wind was turned on. This effect was evident in the series of May 15 with the 5.4 m.p.h. wind, that of May 11 with the 9.5 m.p.h. wind, and those of May 14 and 16 with the 16 m.p.h. wind, but in none of the others. In all cases this effect appeared in about 15 minutes and vanished in about half an hour, and in no case was it very marked. Wind of 16 m.p.h. caused slight bruising around the edges of some of the leaves and in places where they folded over or touched each other; however, this effect was not noticeable with lower velocities.

TABLE IV

VALUES OF AIR TEMPERATURE IN DEGREES FAHRENHEIT AND RELATIVE HUMIDITY IN PERCENTAGE FOR THE SERIES TAKEN INSIDE GREENHOUSE

5/8/35	Time	9:30	11:30	12:30	1:30	2:30	3:30	5:15	8:20	
	Air temp.	74	75	83	86	91	87	78	67	
	Rel. hum.	58	51	47	47	40	41	47	56	
5/9	Time	8:30	9:30	11:30	12:30	1:30	2:30	3:30	5:15	9:30 P.M.
	Air temp.	72	76	77	82	80	77	77	72	65
	Rel. hum.	59	53	54	50	52	52	52	57	68
5/10	Time	8:30	10:15	11:30	12:30	1:30	2:45	3:30	5:15	8:30
	Air temp.	65	73	82	80	76	81	83	78	62
	Rel. hum.	68	57	51	52	55	51	50	53	64
5/11	Time	9:45	11:45	12:30	1:30	1:55	2:30	3:30	5:30	8:30
	Air temp.	84	99	102	108	100	95	84	72	63
	Rel. hum.	51	36	36	33	37	30	37	43	57
5/14	Time	8:30	9:30	10:30	12:00	12:30	2:00	3:30	6:15	8:45
	Air temp.	69	70	78	80	81	81	78	70	61
	Rel. hum.	59	55	46	45	47	47	49	53	63
5/15	Time	9:00	10:20	11:15	12:45	1:45	2:45	3:45	5:30	
	Air temp.	74	80	81	78	86	84	81	84	
	Rel. hum.	58	45	49	51	44	43	44	46	
5/16	Time	8:00	10:00	11:30	12:00	1:20	5:20	6:05	8:20	8:30 A.M.
	Air temp.	72	85	102	95	87	86	80	64	80
	Rel. hum.	55	41	36	31	37	33	39	58	47

The very high initial rate of transpiration that takes place at the onset of wind in the higher range of velocities apparently causes a reduction in the sap content of the leaves as shown by their slightly flaccid appearance at this time and a consequent closure of stomata, both of which factors doubtless play a part in the reduction of the relative transpiration rate that occurs during the second weighing interval. Following this second period, the flaccidity disappears and there usually occurs a rather slow increase in the relative transpiration rate, which continues until the wind ceases. The recovery of turgor in the leaves and the fact that the stomata remain at about the same degree of opening during this period of gradual increase indicate that the rise must be due to a gradual restoration of the sap content of the leaves with resultant increase of transpiration. The fact that this gradual increase exists at all indicates that the closure of the stomata retards transpiration sufficiently to permit recovery of the sap content of the leaves.

On the other hand, an indication that the stomata do not always play a controlling part in regulating transpiration is obtained from the relative transpiration rate immediately after the wind stops. Though there is at this time practically always a reduction in the rate of the test set below that of the control, it is rarely more than 20 per cent., in spite of the fact that the stomatal opening may be considerably less. In this connection it is important to note that even in cases when the stomata are open, a drop of about 10 per cent. occurs, due probably in these cases to the lower sap content of the leaves. This view is supported by the fact that the relative influence of wind on the rate of water loss during the night, when the stomata are closed, is much the same as during the day. This means either that wind has practically the same effect on the cuticular as on the stomatal component of transpiration, or that stomata may sometimes play only a small part in the regulation of transpiration. This latter view is supported by the work of other investigators (**10, 13, 15, 16**).

Comparison of the data from different series indicates that the closure of stomata by wind is not entirely due to the water relations, but at least partly to mechanical action. This is well illustrated by comparison of the stomatal behavior of the test set on May 10 (wind of 5.5 m.p.h.) with that of the control on May 11. In the former case, the stomata closed and remained so while the wind continued, but in the latter they remained wide open, even though the transpiration rate throughout the series was nearly twice as great. A direct test of this assumption is difficult, since it is hard to shake a leaf without increasing its transpiration, and it is also difficult to prevent wind shaking the leaf. This effect is in agreement with the work of KNIGHT (**11**) and LOFTFIELD (**16**), who found that the stomata of some plants are sensitive to the shock of handling the leaves.

Discussion

The assumption that the high initial rise in the transpiration rate that occurs at the onset of winds of velocities greater than about 3 m.p.h. lasts probably less than 15 minutes is supported by the experimental data. The effect is illustrated best by the series of May 16 with the 16 m.p.h. wind. In this series, the transpiration rate for the first 15 minutes after the wind started was 2.08 grams per square decimeter per hour, representing an increase of 100 per cent. with respect to the control, while for the next period, also 15 minutes, the rate was 0.92, or an increase of only 31 per cent. with respect to the control. This large decrease in the relative transpiration rate during the second period indicates that at the beginning of the initial period the increase in the rate of the test set must have been much greater than 100 per cent. and at the end smaller. This assumption is further supported by the fact that at the end of the initial 15-minute period, the leaves showed some evidence of flaccidity even though the transpiration rate was only 2.08 gm./dm.^{2}/hr., while during the period 12:30–1:30 on May 11 the rate of transpiration of the test set was 3.98 with no evidence of flaccidity. This sort of action appears to be explainable only by the assumption that the transpiration rate must be very high for the first few minutes of the initial period of wind with a subsequent rapid decrease. It is unfortunate that the methods used in these experiments did not permit a direct test of this assumption, but 15 minutes was the shortest time interval that could be employed without too great sacrifice of accuracy in weighings.

When the stomata do respond to the action of wind, they close partially or completely, as the case may be, in less than half an hour, and for the high velocities in less than 15 minutes. The lowest velocity of wind that will induce closure of stomata seems to be somewhere between 2 and 3 m.p.h., although some series have been taken in which wind of as high as 5 m.p.h. had no noticeable effect on the stomata. In these, however, there was no indication of the very high initial rise in the relative transpiration rate that occurs in the series given here with the same wind velocity, although the average increase in the rate for the entire period of wind agreed very closely. The range between 2 and 5 m.p.h. appears to be critical in that wind of these velocities will sometimes close stomata, sometimes not, apparently depending upon some factor or factors to which it cannot at present be assigned. Below this range, wind has not been observed to affect the stomata, but above it invariably does so.

II. Effect of wind on growth and transpiration; long time series

Methods

For these experiments, plants of *Helianthus annuus* were grown from seed in cans of the type described above, with three or four seeds in each.

When the plants had reached the first leaf stage, they were selected for uniformity of height and leaf size, leaving only one in each can. The cans were then sealed with sand and cotton, and placed in wooden boxes $2 \times 4 \times 1$ ft. deep, sunk in the ground with their tops level with the surface. These boxes were covered with rather closely fitting lids of masonite in order to prevent the large variations in soil temperature that would occur if the cans were exposed directly to the sun's rays. Four of these boxes were used with six phytometers and one check can in each. One set served as a control with only the natural wind, while the other three had artificial wind of about 5, 10, and 15 miles per hour produced by the fans described above. These fans measure approximately 20 to 22 inches in diameter, so that the stream of air was quite wide enough to cover the entire set of plants throughout the growing period.

The water content was maintained constant within a few per cent. and a record of water used was kept. Measurements of leaf areas and diurnal variations in transpiration rates and stomatal openings were made at intervals during the growing period. When the plants had become as large as the wind current would cover, the series was terminated, final measurements of leaves and stems were made, and the plants were dried in a large oven to obtain their dry weights (**17**).

Of the four series conducted, two were in the fall and two in the spring. Series I began with the planting on September 25, 1933, and ended November 17; the second ran from March 13, 1934, to May 2; the third started September 15, 1934, and ended October 26; and the fourth lasted from February 26, 1935, to April 25.

Results

The average leaf areas of plants taken at intervals during series I are given in table V and are shown graphically in figure 5. The four curves, A, B, C, and D, correspond to the four sets of plants, A, B, C, and D, respec-

TABLE V

AVERAGE LEAF AREAS OF PLANTS IN SQUARE DECIMETERS AT INTERVALS DURING THE GROWING PERIOD; SERIES I

SET NO.	DATE					
	10/16	10/23	10/31	11/7	11/9	11/17
A	1.16	3.58	10.70	19.00	22.20	46.5
B	1.17	3.78	10.20	18.30	21.20	44.5
C	0.83	2.20	5.50	10.90	12.90	26.8
D	0.70	1.92	3.63	6.33	7.33	13.9

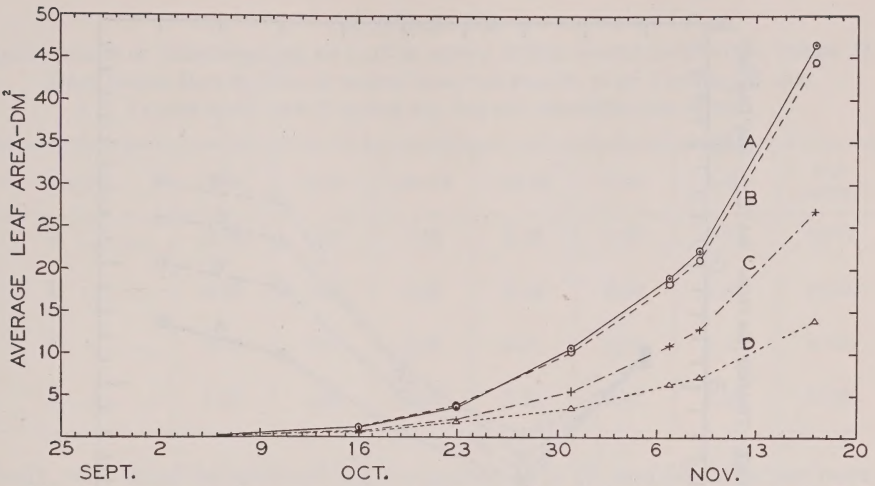

FIG. 5. Average leaf areas in square decimeters for the four sets of plants A, B, C, and D with wind velocities of about 0, 5, 10, and 15 miles per hour respectively, determined at intervals during series I.

TABLE VI

WEEKLY AVERAGE TRANSPIRATION RATES DURING THE GROWING PERIOD FOR SERIES IV

PERIOD	SET NO.	AVERAGE TRANSPIRATION RATE	
		GM./DM.²/24 HR.	PERCENTAGE OF CONTROL
3/20/35	A (control)	11.4	100
to	B	11.4	100
3/27	C	11.0	96
	D	10.9	96
3/27	A	5.94	100
to	B	6.40	108
4/3	C	7.09	119
	D	7.88	133
4/3	A	8.04	100
to	B	9.62	120
4/10	C	10.8	134
	D	10.3	128
4/10	A	11.3	100
to	B	14.0	124
4/17	C	15.9	141
	D	17.5	155
4/17	A	12.6	100
to	B	15.0	119
4/24	C	16.8	133
	D	18.3	145

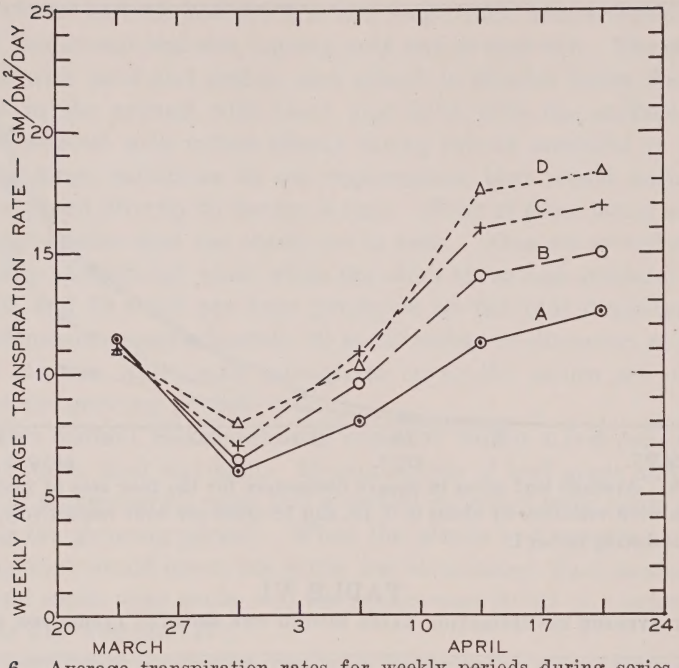

FIG. 6. Average transpiration rates for weekly periods during series IV.

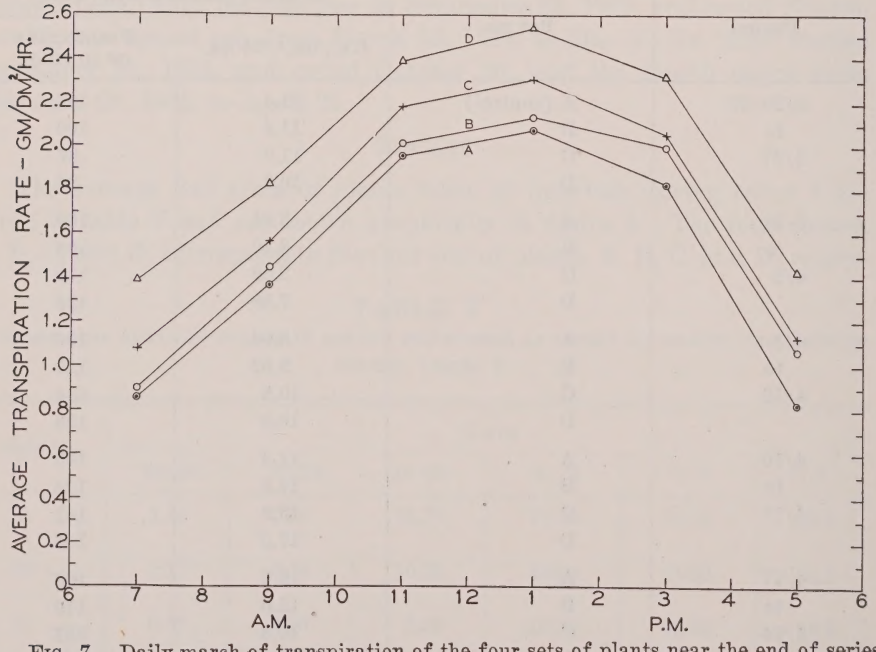

FIG. 7. Daily march of transpiration of the four sets of plants near the end of series II. Data taken May 2, 1934, at which time the plants were 7 weeks of age.

TABLE VII

DAILY MARCH OF TRANSPIRATION OF PLANTS GROWN UNDER CONTINUOUS WIND; SERIES II. DATA TAKEN MAY 2, 1934, AT WHICH TIME THE PLANTS WERE 7 WEEKS OF AGE. VALUES GIVEN ARE IN GRAMS PER SQUARE DECIMETER PER HOUR

SET NO.	6–8	8–10	10–12	12–2	2–4	4–6	6–6 (NIGHT)
A	0.86	1.37	1.96	2.08	1.83	0.83	0.071
B	0.90	1.45	2.02	2.14	2.00	1.07	0.095
C	1.08	1.57	2.19	2.31	2.06	1.13	0.191
D	1.39	1.83	2.39	2.54	2.32	1.43	0.306

tively, with wind velocities of approximately 0, 5, 10, and 15 miles per hour. The average transpiration rates for weekly periods during series IV were obtained from the average leaf areas and total transpiration during those periods; they are given in table VI and are shown graphically in figure 6.

TABLE VIII

RESULTS FROM THE FOUR SERIES

SERIES	SET NO.	AV. LEAF AREA	AV. STEM HT.	AV. STEM DIAM.	AV. DRY WT.	AV. TOTAL TRANSPIRATION	AV. WATER REQUIREMENT	AGE OF PLANTS	NO. PLANTS PER SET
		dm.^{2}	*cm.*	*mm.*	*gm.*	*gm.*	*gm./gm.*	*days*	
	A	46.5	62	14.7	33.5	7520	224		5
I	B	44.5	63	15.0	29.0	6870	237	53	6
	C	26.8	40	11.4	18.5	4960	268		6
	D	13.9	33	10.3	11.2	3210	286		6
	A	28.0	63	13.3	40.0				6
II	B	18.7	47	12.2	28.6			50	4
	C	18.0	45	11.7	26.6				5
	D	13.5	44	11.6	22.4				6
	A	37.0	53	13.9	21.3	4730	222		6
III	B	31.8	42	12.5	19.1	4320	226	41	5
	C	15.5	33	9.8	10.2	2770	271		6
	D	8.5	23	8.6	6.2	1760	284		6
	A	15.4	48	11.3	16.5	2640	160		6
IV	B	14.0	48	11.2	15.8	2765	175	58	6
	C	12.9	47	11.0	12.2	2515	206		6
	D	9.3	32	9.6	7.1	1770	249		5

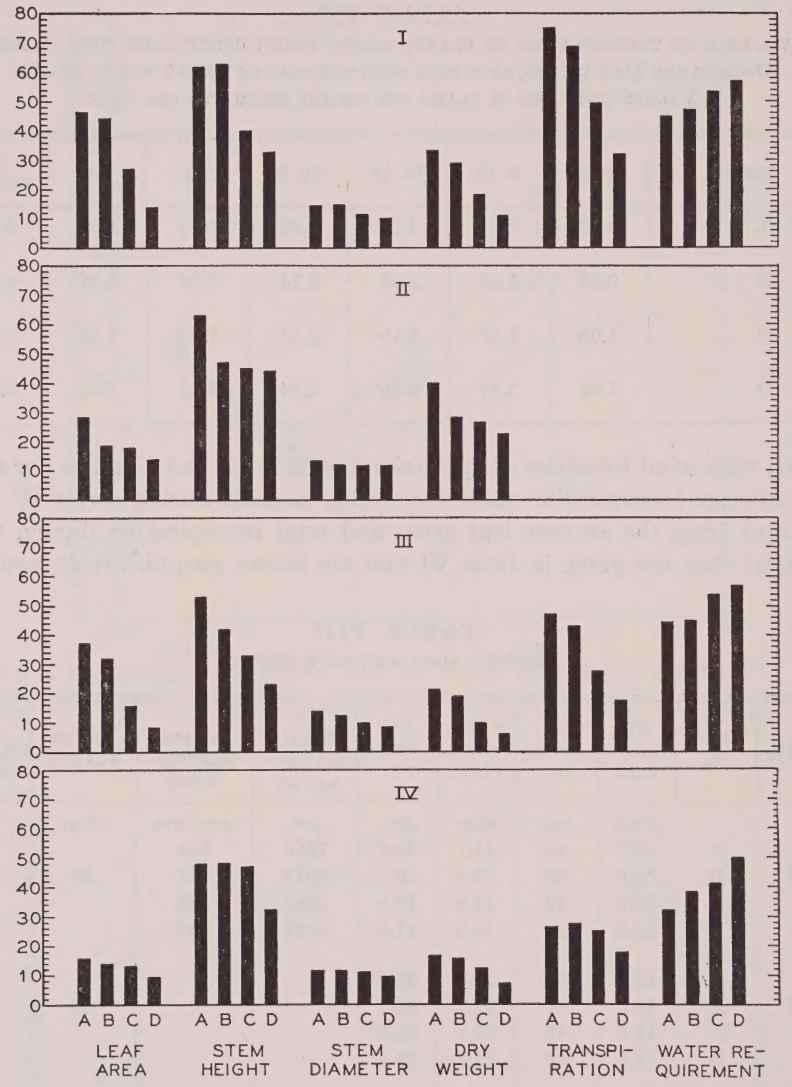

FIG. 8. Final plant measurements, total transpiration, and water requirement for all series. The ordinate represents leaf areas in square decimeters, stem heights in centimeters, stem diameters in millimeters, and dry weight in grams, but only 1/100 of the total transpiration in grams and 1/5 of the water requirement in grams of water per gram dry weight of material produced.

For the first week after subjection to wind, sets A and B had the same transpiration rate, while sets C and D were a little less. Thereafter, however, the transpiration rates per unit area increased with the wind, reaching a maximum for the highest velocities during the last two weeks of the series of from 35 to 50 per cent. more than the control.

The daily march of transpiration near the end of the series is represented by the data from series II given in table VII and shown graphically in figure 7. The transpiration rate at all times of day increased with wind velocity, but the influence is relatively greater at night than during the day. For example, set D (15 m.p.h. wind) at night used water from four to five times as rapidly as the control, while during the day only about 1.4 times. Measurements of stomatal openings during such series showed that for the greater part of the first two weeks the stomata were kept partially closed by the two highest winds, but thereafter wind had no noticeable effect on their diurnal cycle.

The final plant measurements from all four series are given in table VIII and are shown graphically in figure 8. In all series, leaf area, stem height and diameter, dry weight, and total transpiration (with one exception) decreased with increasing wind velocity. Inversely, the water requirement increased, the maximum increment observed being about 50 per cent. in the case of the 15 m.p.h. wind in series IV. The total transpiration and water requirement for series II could not be obtained on account of an unexpected rain that permitted unknown amounts of water to enter the cans.

All series were qualitatively alike in that wind always caused a reduction in growth, although quantitatively there were differences, the greatest being that the effect of wind in the fall seemed to be a little greater than in the spring. In the fall, the 15 m.p.h. wind caused a reduction in dry weight to about one third that of the control, but in the spring to only about one half. Some of the observed differences are doubtless due to statistical fluctuations caused by individual differences, but some are probably caused by diversity in

TABLE IX

WEEKLY AVERAGES OF AIR TEMPERATURE (T) IN DEGREES FAHRENHEIT, AND RELATIVE HUMIDITY (RH) IN PERCENTAGE FOR THE FOUR SERIES

SERIES I			SERIES II			SERIES III			SERIES IV		
WEEK ENDING	T	RH	WEEK ENDING	T	RH	WEEK ENDING	T	RH	WEEK ENDING	T	RH
	°F.	%		°F.	%		°F.	%		°F.	%
10/9/33	62	83	3/19/34	57	87	10/1/34	69	44	3/4/35	51	78
10/16	60	68	3/26	58	86	10/8	62	83	3/11	48	76
10/23	64	53	4/2	64	68	10/15	61	83	3/18	55	75
10/30	57	91	4/9	59	65	10/22	58	89	3/25	48	74
11/6	60	70	4/16	57	85	10/29	60	78	4/1	53	89
11/13	61	52	4/23	58	84				4/8	56	88
11/20	57	77	4/30	65	71				4/15	54	86
									4/22	57	87
			5/7	64	69				4/29	59	80

other environmental factors, thus altering the effect of wind. Weekly averages of air temperature and relative humidity during the four series are given in table IX.

The response of an average plant from each of the four sets in series III, arranged in order of increasing wind velocity, is shown by figure 9. Winds of 10 and 15 m.p.h. caused the well known gnarled and stunted appearance that is characteristic of trees growing in windy habitats. The leaves were rougher, fewer, more wrinkled, and somewhat less fully expanded than those of the control. The number of stomata per unit area rose with increasing wind velocity and the corresponding failure of the leaf to expand, a count for series IV yielding 188, 199, 260, and 304 per square millimeter for sets A, B, C, and D respectively. Microscopic sections of the leaves,

FIG. 9. Typical plants from the four sets in series III. Sets A, B, C, and D, with wind velocities of about 0, 5, 10, and 15 miles per hour respectively, are represented in order from left to right.

however, failed to show any material differences in the mesophyll, owing evidently to compensation by change of size. The stems, on the other hand, showed considerable divergence, particularly in the xylem elements. Camera lucida drawings of quadrants of the four stems, with only the xylem and bast strands outlined, are shown in figure 10. Stems of plants grown under the 15 m.p.h. wind (set D) showed 22 members of the first rank of bundles and only 6 of the second, while those of the control (set A) exhibited 22 of the first, 22 of the second, and 7 of the third. The intermediate sets fell between these two extremes. Although the number of members of the first rank of bundles was the same for both sets A and D, the number of vessels in each bundle was quite different. Each first rank bundle of A was made up of about 50 vessels while those of the same rank in D had only 30. Similarly, the area occupied by the xylem was considerably larger in A than in D, the former being 3.87 mm.^{2}, the latter 1.20. The cross-section area of the stems A and D were 113.0 and 36.6 mm.^{2}, respec-

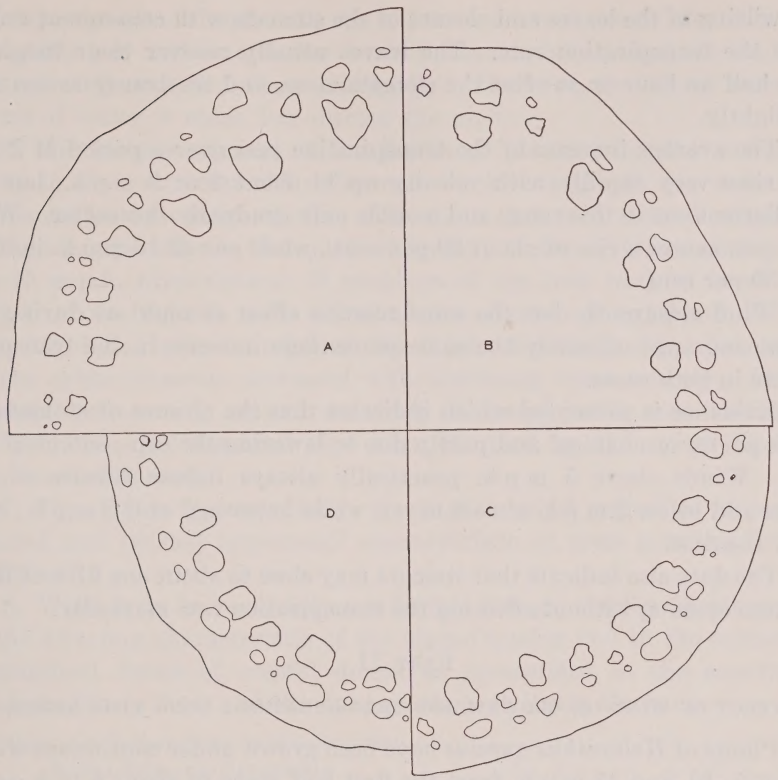

FIG. 10. Camera lucida drawings of quadrants of stems from typical plants from each of the four sets in series IV, with only the xylem and bast strands outlined.

tively; hence the proportion of the total stem area occupied by the xylem was practically the same in both cases, being 3.4 per cent. in the former and 3.3 in the latter.

Summary

PART I

EFFECT OF WIND ON TRANSPIRATION; SHORT TIME SERIES

1. The effect of wind on the transpiration rate of *Helianthus annuus* depends on the velocity. With velocities up to about 2 m.p.h., the transpiration rate increases at the onset of wind about 20 to 30 per cent. and maintains this value as long as the wind acts. For velocities above this, however, there is usually a rather high relative increase for the first few minutes after the wind is turned on, followed by a fall, which in turn is followed by a gradual increase. The initial increase in the rate of water loss rises with increasing velocity, reaching 138 per cent. in the case of the 16 m.p.h. wind. This causes

slight wilting of the leaves and closure of the stomata with consequent reduction in the transpiration rate. The leaves usually recover their turgidity within half an hour or so after the stomata close, and the transpiration rate rises slightly.

2. The average increase of the transpiration rate over a period of 2 to 4 hours rises very rapidly with velocity up to about 2 or 3 m.p.h., but the curve flattens out in this range and mounts only gradually thereafter. Wind of 1 m.p.h. causes a rise of about 30 per cent., while one of 16 m.p.h. induces about 50 per cent.

3. Wind apparently has the same relative effect at night as during the day, causing approximately the same percentage increase in the transpiration rate in both cases.

4. Evidence is presented which indicates that the closure of stomata by wind is partly mechanical and partly due to lowering the sap content of the leaves. Winds above 5 m.p.h. practically always induce closure of the stomata and below 2 m.p.h. almost never, while between 2 and 5 m.p.h., only part of the time.

5. The data also indicate that stomata may close to about one fifth of their maximum opening without affecting the transpiration rate markedly.

Part II

Effect of wind on growth and transpiration; long time series

1. Plants of *Helianthus annuus* have been grown under continuous winds of about 5, 10, and 15 m.p.h. from the first leaf stage to about 6 to 8 weeks of age, using large automobile fans driven by electric motors. Four series were made, two in the spring, two in the fall.

2. For the first week the transpiration rates of all three test sets were practically the same as that of the control, but thereafter the rate began to increase with increasing wind velocity so that by the end of the series the three test sets were using water at rates about 20, 35, and 50 per cent. higher per unit area of leaf surface than the control.

3. In all series, leaf area, stem height and diameter, dry weight, and total transpiration decreased with increasing wind velocity. The water requirement increased, the maximum increment observed being about 50 per cent. in the case of the 15 m.p.h. wind in series IV.

4. The depressing effect of wind on growth appears to be somewhat greater in the fall than in the spring. In the former cases, wind of about 15 m.p.h. caused a reduction in dry weight to about one third that of the control, but in the spring to only approximately one half.

5. In these series, the effect of wind on the transpiration rate is relatively considerably greater during the night than during the day. During

the day, the plants under the 15 m.p.h. wind transpired about 1.5 times as rapidly per unit area as the control plants, while during the night they transpired from 4 to 5 times as rapidly. However, the actual increase in grams of water is much less during the night.

6. Microscopic sections of the leaves of plants from the various sets failed to show any material differences in the mesophyll, due evidently to compensation by change of size. The stems, however, showed considerable difference, especially in the xylem elements. Stems of plants grown under the 15 m.p.h. wind showed 22 members of the first rank of bundles and only 6 of the second, while those of the control set exhibited 22 of the first, 22 of the second, and 7 of the third. Similarly, the area occupied by the xylem elements decreased with increasing wind velocity. However, the total cross-section area of the stems decreased in the same ratio so that the proportion of the total stem area occupied by the xylem showed no significant difference.

7. The plants grown under the higher wind velocities showed the gnarled and twisted appearance characteristic of trees growing in windy habitats.

8. Wind is to be regarded as a factor, though not the paramount one, in the dwarfing characteristic of the alpine tundra and in the reduced and procumbent forms of coastal dunes, as exemplified in the experimental areas on Pike's Peak and the dune gardens at Santa Barbara.

CARNEGIE INSTITUTION OF WASHINGTON
SANTA BARBARA, CALIFORNIA

LITERATURE CITED

1. BLANCHARD, V. F. Depressing effect of wind on growth and yield of citrus trees. California Citrogr. **19**: 206–207. 1934.
2. BRIGGS, L. J., and SHANTZ, H. L. Daily transpiration during the normal growth period and its correlation with the weather. Jour. Agr. Res. **7**: 155–212. 1916.
3. ————————, ————————. Hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agr. Res. **5**: 583–650. 1916.
4. BROWN, M. A. The influence of air currents on transpiration. Iowa Acad. Sci. Proc. **17**: 13–15. 1910.
5. CLEMENTS, F. E., and GOLDSMITH, G. W. The phytometer method in ecology. Carnegie Inst. Washington Publ. no. 356. 1924.
6. COPELAND, E. B. On the water relations of the cocoanut palm. Phil. Jour. Sci. **1**: 6–57. 1906.
7. FINNELL, H. H. Effect of wind on plant growth. Jour. Amer. Soc. Agron. **20**: 1206–1210. 1928.

8. Firbas, F. Die Wirkung des Windes auf die Transpiration. Ber. deutsch. bot. Ges. **49**: 443–452. 1931.
9. Giddings, L. A. Transpiration of *Silphium laciniatum* L. Plant World **17**: 309–328. 1914.
10. Jeffreys, H. Some problems of evaporation. Phil. Mag. Jour. Sci. 6th ser. **35**: 270–280. 1918.
11. Knight, R. C. Recent work on transpiration. New Phytol. **16**: 127–139. 1917.
12. ————. "Relative transpiration" as a measure of the intrinsic transpiring power of the plant. Ann. Bot. **31**: 351–359. 1917.
13. ————. The interrelations of stomatal aperture, leaf water-content, and transpiration rate. Ann. Bot. **31**: 221–240. 1917.
14. Lloyd, F. E. The physiology of stomata. Carnegie Inst. Washington Publ. no. 82. 1908.
15. ————. The relation of transpiration and stomatal movements to the water-content of the leaves in *Fouquieria splendens*. Plant World **15**: 1–14. 1912.
16. Loftfield, J. V. G. The behavior of stomata. Carnegie Inst. Washington Publ. no. 314. 1921.
17. Martin, E. V. A large-capacity drying oven with constant uniform temperature and forced ventilation. Plant Physiol. **9**: 689–692. 1934.
18. Seybold, A. Weitere Beiträge zur Kenntnis der Transpirationsanalyse. Planta **13**: 18–28. 1931; **14**: 77–93, 386–410. 1931; **16**: 518–525. 1932.
19. ————. Die pflanzliche Transpiration. Ergebn. Biol. **5**: 29–165. 1929.
20. ————. Zur Klärung des Begriffes Transpirationswiderstand. Planta **21**: 353–367. 1933.
21. Stålfelt, M. G. Der Einfluss des Windes auf die kutikuläre und stomatäre Transpiration. Svensk Bot. Tidsk. **26**: 45–69. 1932.
22. Wilson, H. W. Studies on the transpiration of some Australian plants. Roy. Soc. Victoria Proc. **36**: 175–237. 1924.

Reprinted from PLANT PHYSIOLOGY, 10: 341–354, 1935.

EFFECT OF SOLAR RADIATION ON TRANSPIRATION OF *HELIANTHUS ANNUUS*

EMMETT V. MARTIN

Introduction

Considerable attention has been given to radiant energy as a factor in the rate of transpiration. Although the early investigations were for the most part qualitative in character, all demonstrated the strong accelerating action of radiation. BRIGGS and SHANTZ (**4, 5**) have made extensive observations of the daily march of transpiration and environmental factors, and have found a high degree of correlation between water loss and radiation. Recently, ARTHUR and STEWART (**2**) have measured the rate of transpiration of *Nicotiana tabacum* under controlled conditions in the laboratory, and find that to double the radiation increases the rate of water loss approximately 1.7 times. However, an attempt to separate the effect of radiation from that of other environmental factors by means of measurements taken under natural conditions has never been made. From the point of view of the ecologist analyzing the factor complex, such determinations are of considerable value. In an experiment of this sort, it is necessary to change the amount of radiation received by the plants without materially altering the other environmental factors. These conditions were fulfilled in the present work by the use of specially constructed shade tents that transmit different amounts of radiation but allow such freedom of air circulation that the other factors are not appreciably affected.

Methods

In these experiments two types of shade tents were employed. The first consisted of a plane framework of wood 3 feet square covered with cloth, the weave and number of layers determining the intensity of radiation transmitted. These screens were supported at a distance of 1 to 2 feet from the plants and were moved every few minutes during a series so as to maintain the plants in shadow. The second type was somewhat more elaborate in design, as shown in figure 1. The main arch is a 20-foot piece of 3-inch redwood batten bent into the form of a semicircle, while the lower arch is 10 feet long and of similar curvature. The centers of these two pieces are connected by a 4-foot piece of ½-inch iron rod and their ends by 6-foot pieces of batten. This structure is supported with the main arch in an east-west line by five stakes driven in the ground, one at each end of the 6-foot crosspieces and one at the center of the lower arch.

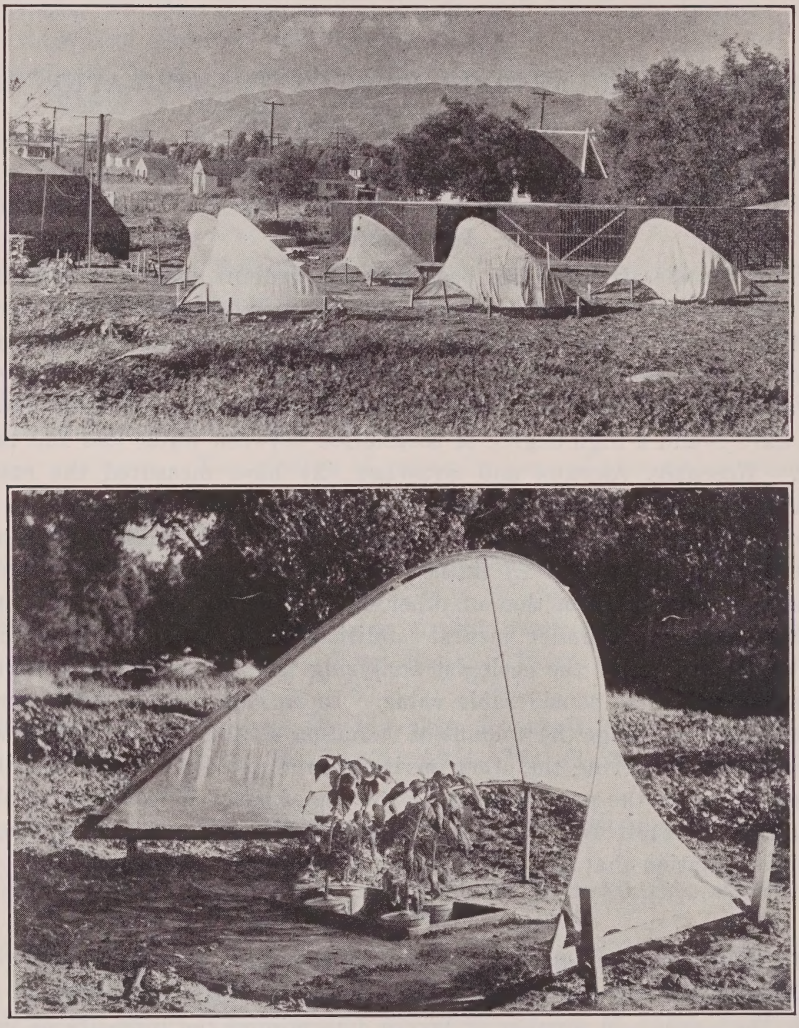

FIG. 1. Above, distant view of entire group of tents; below, close-up view of tent *D*.

Five of these tents were used, each covered with a different type and thickness of cloth as follows: *B* with one layer of cheesecloth with a thread count of 20×16; *C* with one 28×24; *D* with one each of 20×16 and 36×32; *E* with one layer of sheeting 56×60; and *F* with two layers of medium-weight white canvas. The iron rod across the center of each tent was removable, thus permitting the tents to collapse when not in use, a feature that was found to be necessary for even moderately windy days. A wooden box, 4 feet long, 2 feet wide, and 1 foot deep, to hold the phy-

tometers, was sunk in the ground in the center of the space covered by the tent, with its long side in an east-west line. During the fall and winter months, these tents cast the desired shadow all day; but for use in summer, they would need to be constructed differently.

For some of the series, plants of *Helianthus annuus* were grown from seed in water-tight, cylindric, galvanized iron cans 8 inches in diameter and 10 inches in height, while for others similar cans $8\frac{1}{2} \times 11$ inches were employed. Each of these was fitted with a removable lid that had in its center a circular opening 2 inches in diameter. The soil used was a good loam of as nearly uniform texture and moisture as was feasible. The holard was set at approximately 65 per cent. of saturation (or 28 per cent. of the dry weight of the soil), and the total amount of water in each can was kept within 15 per cent. of this value throughout the growing period; and during all series it was maintained constant within 3 per cent. When necessary, water was added through a glass tube extending into a layer of gravel about 1 inch thick in the bottom of the cans. When the plants were a few weeks old, the containers were sealed by adding a layer of sand about $\frac{3}{4}$ inch thick on top of the soil, filling the opening in the lid with non-absorbent cotton, and corking the glass tube. The efficiency of this type of seal was tested by means of controls without plants. Weighings made on a torsion balance to the nearest gram during the time the experiments were in progress showed that such containers seldom lost a detectable amount. This seal has an advantage over the paraffin type in that forced aeration is unnecessary (CLEMENTS and GOLDSMITH **6**).

In all series, six sets of from four to six plants each were used, one set under each tent and a control group in the open, the plants in each set being arranged so as not to shade one another. For the whole-day series the plants were placed under the tents before sunrise and weighed every hour throughout the day. For the short series the plants were put in position about half an hour before the first weighing, which was usually about ten or eleven o'clock in the morning, allowed to remain undisturbed for two to four hours (the time depending upon weather conditions), and again weighed. On account of the fact that clouds cause such rapid fluctuations in radiant energy, series could be run only during periods of cloudless skies. Measurements of air temperature, relative humidity, and average wind velocity were taken every hour during all series. Leaf areas in square decimeters were determined by multiplying the product of the length and width of the leaves in centimeters by the factor 0.0134 (**6**).

Measurements of solar radiation intensity under each tent and in the open were taken two or three times each hour by means of the Smithsonian pyranometer (**1**), which records the intensity of radiation (direct plus diffuse) falling on a horizontal surface. The average intensity during a series

was determined by plotting the observed values on cross-section paper, connecting consecutive points by straight lines as in figure 3, reading the values from this graph for every ten or fifteen minutes, and averaging them.

Results

The transpiration data and radiation measurements for the whole-day series of November 2, 1934, are given in tables I and II respectively, and

TABLE I

TRANSPIRATION DATA OF NOVEMBER 2, 1934

TIME		TENT					
		A (CONTROL)	B	C	D	E	F
A. M.	W*=	30	27	47	20	25	23
7–8	t =	0.98	0.97	0.95	0.93	0.90	0.87
	T =	0.27	0.27	0.41	0.19	0.28	0.27
	W =	118	97	105	67	64	54
8–9	t =	0.90	0.92	0.90	0.90	0.90	0.92
	T =	1.14	1.02	0.96	0.86	0.71	0.59
	W =	203	136	154	109	83	65
9–10	t =	1.00	0.98	0.98	0.97	0.98	0.97
	T =	1.77	1.35	1.30	0.99	0.85	0.68
	W =	252	198	205	161	131	103
10–11	t =	1.03	1.05	1.08	1.10	1.08	1.10
	T =	2.12	1.83	1.57	1.30	1.21	0.95
	W =	270	220	229	183	145	115
11–12	t =	1.02	1.02	1.00	1.00	1.00	1.00
	T =	2.30	2.09	1.89	1.62	1.45	1.16
P. M.	W =	323	253	269	225	177	148
12–1	t =	1.18	1.18	1.18	1.18	1.18	1.18
	T =	2.38	2.08	1.88	1.69	1.50	1.27
	W =	224	189	199	161	128	105
1–2	t =	0.88	0.87	0.85	0.83	0.82	0.82
	T =	2.22	2.11	1.94	1.72	1.56	1.29
	W =	275	233	257	213	174	142
2–3	t =	1.02	1.02	1.03	1.05	1.08	1.12
	T =	2.34	2.22	2.06	1.80	1.61	1.28
	W =	222	179	179	153	110	90
3–4	t =	1.02	1.02	1.02	1.03	1.03	0.98
	T =	1.89	1.70	1.45	1.31	1.07	0.93
	W =	81	60	63	52	42	33
4–5	t =	0.95	0.93	0.95	0.93	0.90	0.93
	T =	0.74	0.63	0.55	0.50	0.47	0.36

* W, water loss in grams per set of five plants; t, time interval between weighings in hours; T, transpiration rate in grams per square decimeter leaf area per hour. The leaf areas in square decimeters for the six sets are: A = 115, B = 103, C = 121, D = 113, E = 100, and F = 99.

TABLE II

MEASUREMENTS OF TOTAL RADIATION INTENSITY ON NOVEMBER 2, 1934*

TIME	TENT					
	A (CONTROL)	B	C	D	E	F
7:00– 7:06	0.032	0.032	0.029	0.029	0.028	0.023
7:57– 8:05	0.413	0.239	0.275	0.080	0.092	0.044
8:29– 8:38	0.557	0.441	0.394	0.216	0.119	0.049
8:50– 8:59	0.652	0.487	0.440	0.251	0.136	0.051
9:24– 9:32	0.77	0.607	0.492	0.315	0.151	0.054
9:52– 9:59	0.83	0.65	0.537	0.314	0.156	0.054
10:22–10:32	0.93	0.73	0.571	0.349	0.167	0.057
10:52–11:00	0.99	0.77	0.66	0.371	0.177	0.061
11:29–11:37	1.02	0.78	0.67	0.372	0.182	0.061
11:52–12:01	1.01	0.74	0.66	0.396	0.172	0.061
12:31–12:38	0.99	0.73	0.60	0.406	0.168	0.061
1:05– 1:14	0.88	0.70	0.548	0.381	0.158	0.061
1:41– 1:48	0.81	0.583	0.504	0.354	0.146	0.061
1:59– 2:05	0.77	0.573	0.480	0.342	0.139	0.058
2:28– 2:37	0.68	0.494	0.405	0.273	0.138	0.051
2:58– 3:07	0.568	0.407	0.355	0.244	0.122	0.044
3:37– 3:43	0.360	0.248	0.204	0.163	0.091	0.039
4:03– 4:08	0.216	0.168	0.126	0.117	0.065	0.032
4:35– 4:41	0.037	0.037	0.031	0.055	0.032	0.021
5:01–	0.008	.....	.....	.....	.....	.....

* Values of total radiation intensity are in calories per square centimeter per minute.

are represented graphically in figures 2 and 3. In both figures curve A

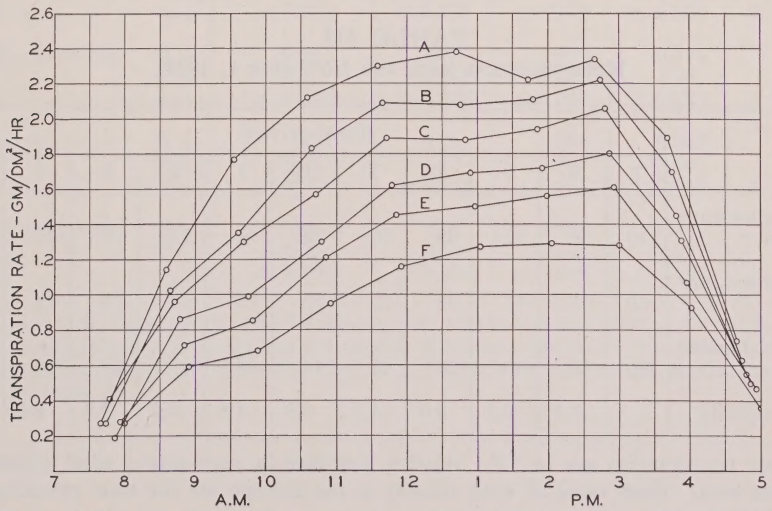

FIG. 2. Transpiration rates for series of November 2, 1934: Curve A corresponds to the open-air control and curves B to F to tents *B* to *F* respectively.

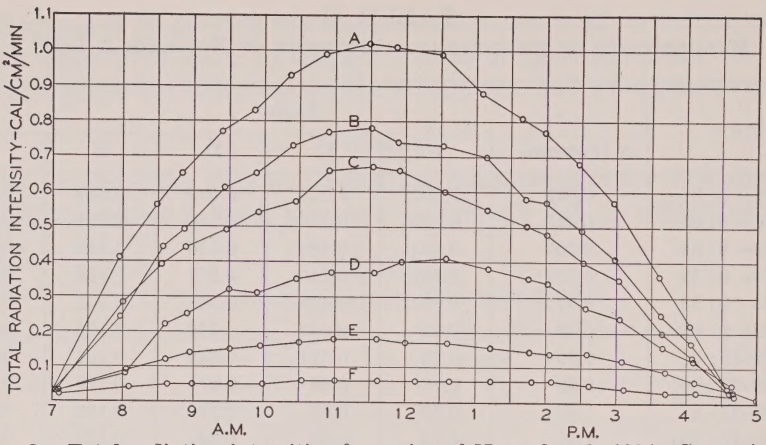

FIG. 3. Total radiation intensities for series of November 2, 1934: Curve A corresponds to the open-air control and curves B to F to tents *B* to *F* respectively.

corresponds to the open-air control and curves B to F to tents *B* to *F* respectively. The transpiration curves for all six conditions are similar in the course of their daily march, but the absolute values decrease with lower radiation. The daily march is controlled by the variations in radiation and meteorological factors throughout the day; but while the radiation differs considerably for the various tents, the other factors are practically identical. Air temperature in the open rarely varied more than 1° from that under tent *F*, as can be seen in table III, while the averages for the two agreed very closely. The construction of the tents being such as to permit fairly free circulation of air, relative humidity and wind velocity

TABLE III

METEOROLOGICAL DATA FOR NOVEMBER 2, 1934

	Time of day										
	7	8	9	10	11	12	1	2	3	4	5
Air temperature (open)*	50	61	67	68	70	72	74	75	76	75	68
Air temperature (tent *F*)	50	61	67	68	71	73	75	75	75	74	67
Relative humidity	80	58	45	53	40	46	43	40	34	30	46
Wind velocity	.....	0.1	0.1	0.5	3.3	3.8	4.8	3.3	3.8	4.8	0.6

* Air temperatures are in ° F.; relative humidity in percentage; wind velocity in miles per hour. Each value of wind velocity is the average for the hour preceding the time of day for which it is given.

TABLE IV

RADIATION AND TRANSPIRATION DATA FOR SHORT SERIES

DATE	TIME LIMITS		TENT					
			A (CONTROL)	B	C	D	E	F
4/21/33	10: 00–2: 30	R* =	1.36	1.04	0.81	0.576	0.343	0.144
		T =	1.76	1.43	1.18	1.01	0.66	0.55
		r_T =	± 0.035	± 0.060	± 0.034	± 0.049	± 0.040	± 0.020
5/13/33	12: 15–3: 00	R =	1.32	1.00	0.82	0.550	0.355	0.143
		T =	1.66	1.29	1.21	1.07	0.93	0.66
		r_T =	± 0.044	± 0.038	± 0.032	± 0.041	± 0.020	± 0.031
3/27/34	10: 45–3: 00	R =	1.09	0.74	0.61	0.454	0.257	0.130
		T =	2.21	1.69	1.58	1.38	1.17	0.93
		r_T =	± 0.032	± 0.029	± 0.038	± 0.021	± 0.022	± 0.020
3/31/34	10: 30–3: 00	R =	1.26	0.87	0.75	0.475	0.273	0.082
		T =	2.74	2.41	2.32	1.92	1.63	1.34
		r_T =	± 0.061	± 0.062	± 0.071	± 0.046	± 0.059	± 0.035
8/1/34	9: 15–11: 00	R =	1.45	1.15	0.96	0.75	0.529	0.058
		T =	2.12	1.95	1.85	1.61	1.36	0.99
		r_T =	± 0.076	± 0.037	± 0.036	± 0.045	± 0.021	± 0.034
8/9/34	10: 30–1: 30	R =	1.40	1.13	0.79	0.494	0.205	0.061
		T =	4.90	4.70	4.45	3.92	3.30	3.14
		r_T =	± 0.112	± 0.132	± 0.107	± 0.026	± 0.133	± 0.098
8/11/34	10: 00–11: 45	R =	1.39	1.06	0.71	0.415	0.208	0.086
		T =	3.86	3.61	3.01	2.75	2.69	2.58
		r_T =	± 0.031	± 0.175	± 0.108	± 0.021	± 0.058	± 0.078
10/11/34	10: 15–3: 15	R =	0.94	0.72	0.570	0.374	0.198	0.088
		T =	2.75	2.28	2.09	1.90	1.62	1.33
		r_T =	± 0.045	± 0.028	± 0.043	± 0.031	± 0.039	± 0.032
10/22/34	11: 00–3: 15	R =	0.93	0.63	0.592	0.348	0.157	0.059
		T =	2.23	1.77	1.85	1.40	1.16	1.08
		r_T =	± 0.115	± 0.045	± 0.055	± 0.042	± 0.036	± 0.051
11/2/34	11: 00–3: 15	R =	0.87	0.65	0.526	0.345	0.150	0.055
		T =	2.31	2.13	1.94	1.71	1.53	1.25
		r_T =	± 0.040	± 0.009	± 0.032	± 0.051	± 0.033	± 0.037

* R, average radiation intensity in calories per square centimeter per minute for period between weighings; T, average transpiration rate in grams per square decimeter per hour for same period; r_T, probable error in T calculated from values given by the various individuals in each set of plants (number of plants in each set is shown in table V).

likewise showed very little difference, so that only the values of these factors obtained from measurements in the open are given in the table.

The transpiration and radiation data for the short series are recorded in table IV, while meteorological and other data are included in table V. The series of August 1 was run at Windy Point, elevation 12,000 feet, on the slopes of Pike's Peak; those of August 9 and 11 at Colorado Springs, Colorado, elevation 6000 feet; and all others at Santa Barbara, California, practically at sea level. The results from five of these series are shown graphically in figure 4, which portrays transpiration rate as a function of

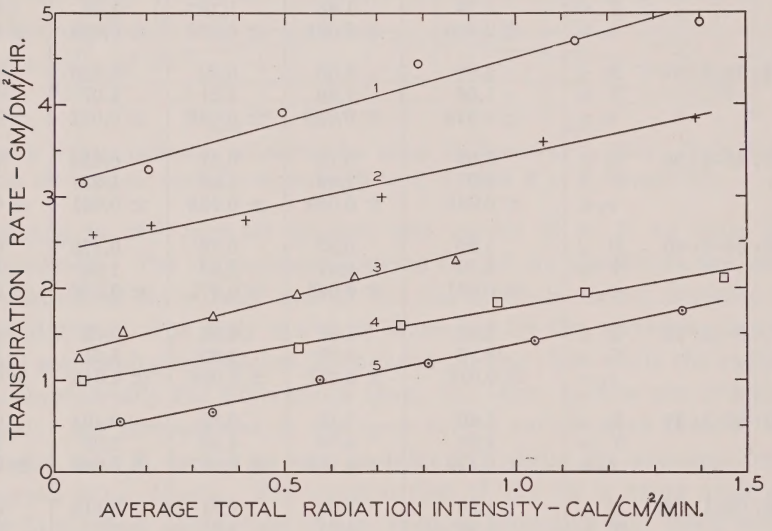

FIG. 4. Results of short series of April 21, 1933 (5), August 1, 1934 (4), August 9, 1934 (1), August 11, 1934 (2), and November 2, 1934 (3).

radiation intensity. Curve 1 represents the data of August 9, curve 2 those of August 11, curve 3 those of November 2, curve 4 those of August 1, and curve 5 those of April 21. In all cases, not only does the rate of transpiration increase with higher intensity of radiation, but the rate of increase is linear. Accordingly the data from all short series are best represented graphically by straight lines, or mathematically by equations of the type $T = b + mR$, where T is the rate of transpiration, R the radiation intensity, b the intercept on the T axis, and m the slope of the straight line. From the point of view of the plant, b should represent the transpiration rate as determined by the combined action of all factors other than radiation, while m should be a measure of the direct effect of the latter.

The method of least squares (various texts, and BIRGE 3) was employed in obtaining from the various series the values of b and m and their probable errors (table V). Both m and b were found to vary considerably for

the different series. Since b is influenced by several factors, it does not show a high degree of correlation with any particular one. In general, however, it increases with higher evaporating power of the air; m, on the other hand, does not vary in the same manner as b. This is readily discernible from table V, but is also clearly shown by the data from the whole-day series of November 2. If the average transpiration rates and radiation intensities for the period 8–9 are used, the value of b is found to be 0.406 ± 0.012 and that of m is 1.203 ± 0.037. Similarly, the data for the period 12–1 yield $b = 1.200 \pm 0.027$ and $m = 1.194 \pm 0.046$. The former is distinctly different for the two periods, while the latter remains constant; hence m is apparently not affected by changes in environmental factors such as take place during the day. On this basis the observed changes in m for different days must be ascribed to some factor or factors in which changes from day to day take place. Two outstanding examples of these are size and age of plants. There appears to be no correlation between average leaf area and m, but there does seem to be a definite relation with age, which is graphically shown in figure 5. Both m and the rate of change of m with age decrease with increasing age. Of the ten points plotted,

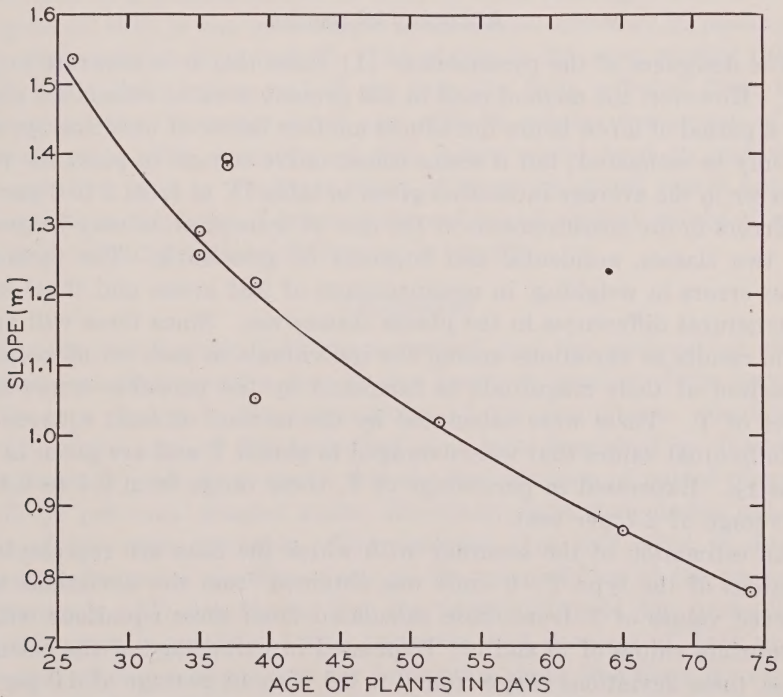

FIG. 5. Slope of transpiration rate *vs.* radiation intensity curves as a function of age of plants in days.

only two are off the curve by more than their probable errors, and these by only twice that amount.

An indication of the importance of radiant energy as a factor in transpiration is furnished by the ratio $mR/(mR+b)$, which gives the fraction of the rate of water loss that is ascribable to the direct effect of radiation. Since this ratio is influenced by a number of factors, it varies over a wide range of values and is usually larger on cold humid days than on warm dry ones. Under the conditions in these experiments, it varied from 38 to 81 per cent., but under more extreme conditions a greater range could be expected.

Leaf temperatures of the plants in the open and under tent *F* were taken at noon for three of the series by means of the well known thermocouple method (7). The temperature of leaves hanging nearly at right angles to the sun's rays in the open averaged about 1° C. above that of the air, while that of leaves under tent *F* was about 5° C. below. These temperatures, however, fluctuated so much with air currents and for different leaves on the same plant that no attempt was made to obtain the average for entire plants under the various conditions.

Accuracy of results

The designers of the pyranometer (1) claim that it is accurate to 1 per cent. However, the method used in the present work to obtain the average over a period of a few hours introduces another factor of uncertainty, which can only be estimated; but it seems conservative enough to place the probable error in the average intensities given in table IV at from 2 to 3 per cent.

Errors in the measurements of the rate of transpiration may be grouped into two classes, accidental and constant or systematic. The former includes errors in weighing, in measurements of leaf areas, and those caused by structural differences in the plants themselves. Since these will appear in the results as variations among the individuals in each set of plants, an estimation of their magnitude is furnished by the probable errors in the values of T. These were calculated by the method of least squares from the individual values that were averaged to obtain T and are given in table IV as r_T. Expressed in percentage of T, these range from 0.4 to 6.1 with an average of 2.7 per cent.

An estimation of the accuracy with which the data are represented by equations of the type $T = b + mR$ was obtained from the deviations of the observed values of T from those calculated from these equations with the appropriate values of m and b. Expressed in percentage of the calculated values, these deviations range from 0 to 8.3 with an average of 3.0 per cent. Since these are of the same order of magnitude as the probable errors in T, the relation between rate of transpiration and intensity of radiation can

be considered linear within the limits of experimental error. These deviations are responsible for uncertainty in the values of b and m, given in table V with their probable errors which in the case of b range from 2.2 to 6.2 with an average of 3.5 per cent., and in the case of m from 2.8 to 7.0 with an average of 4.8 per cent.

The second class of errors (constant or systematic) includes those caused by such factors as stomatal opening, time required to weigh the entire group of plants, and differences in the quality of radiation under the various tents. The degree of opening of the stomata of each set of plants was determined at hourly intervals during the whole-day series and most of the short ones by means of the alcohol method (**10**), but at no time was any appreciable difference found. The uncertainty introduced by the time taken to weigh the entire group of plants (20 to 25 minutes) has been discussed in an earlier paper (7) and shown to be negligible under the conditions of these experiments.

IVANOV and THIELMAN (9) have shown that the rate of transpiration of potted plants may be 50–60 per cent. greater under blue-violet than under red-yellow light of the same intensity. Accordingly this factor must be considered as a possible source of error in these investigations, since there is a gradual shift in the wave length of maximum intensity in passing from open air condition *A* to tent *F*. The plants in the open receive full sunlight, while those under tent *F* get only the light reflected from nearby objects and that from the north sky with its greater proportion of short wave lengths. The operation of this factor would tend to increase the transpiration rates in the lower range of intensity, which would appear in the results in the form of larger values of b and smaller values of m than would be obtained with no differences in quality.

Discussion

LECLERC DU SABLON (**11**) has suggested that the accelerating effect of radiation on transpiration may be due partly to heating of the leaves and partly to a change in the permeability of the protoplasm. Confirmation of the second part of this hypothesis has been furnished by IVANOV and THIELMAN (9), who have shown that the transpiration of potted plants may be 50–60 per cent. greater under blue-violet light than under red-yellow light of the same intensity. They suggest that this effect is due to a greater influence of the blue-violet on the permeability of the protoplasm. LEPESCHKIN (**12**) has shown that the permeability of the protoplasm of *Elodea* leaves to methylene blue increases with increase of light up to 10 per cent. of full sunlight, but for intensities above this there is very little, if any, change. Since practically all the intensities used in the present work are above this value, it may be that change of permeability plays a

TABLE V

ADDITIONAL DATA FOR SHORT SERIES

DATE	AV. AIR TEMP.	AV. REL. HUMIDITY	AV. WIND VELOCITY	AIR PRESSURE	AGE OF PLANTS	AV. LEAF AREA PER PLANT	TYPE OF TENT	PLANTS PER SET	b*	m*
	°F.	*%*	*m.p.h.*	*cm. Hg*	*days*	*dm.²*				
4/21/33	66	51	1.8	76	52	11.9	Sq.	4	0.372 ± 0.023	1.018 ± 0.029
5/13/33	64	53	2.6	76	74	14.1	Sq.	4	0.595 ± 0.034	0.779 ± 0.043
3/27/34	71	62	1.9	76	35	13.2	Arc	6	0.808 ± 0.023	1.255 ± 0.036
3/31/34	74	41	1.7	76	39	18.6	Arc	6	1.306 ± 0.042	1.216 ± 0.058
8/ 1/34	62	41	2.0	49	65	6.0	Sq.	4	0.937 ± 0.034	0.865 ± 0.036
8/ 9/34	86	31	7.6	61	37	5.7	Sq.	4	3.123 ± 0.081	1.393 ± 0.097
8/11/34	82	41	1.8	61	39	6.8	Sq.	4	2.402 ± 0.053	1.051 ± 0.067
10/11/34	76	53	1.6	76	26	6.8	Arc	6	1.254 ± 0.041	1.534 ± 0.073
10/22/34	73	48	1.6	76	37	25.3	Arc	4	0.956 ± 0.029	1.383 ± 0.054
11/ 2/34	73	41	3.9	76	35	21.7	Arc	5	1.254 ± 0.034	1.289 ± 0.066

* Values of b and m given are accompanied by their probable errors calculated by the method of least squares.

minor rôle in the results, and that the accelerating action of radiation observed is due largely to its heating effect. No estimate of the relative magnitude of the effects of these two factors was obtained in these experiments, since it would require knowledge of air and leaf temperature differences as well as of the amount of radiant energy absorbed by the leaves, both of which are much too variable under natural conditions to be measured accurately. The fact that the relation between radiation and transpiration is linear, however, indicates that any change of permeability that may exist under the conditions in these tests will be either small in comparison to the heating effect or directly proportional to the intensity of radiation.

Similarly, the cause or causes of the variation of the accelerating effect of radiation with age of the plants (fig. 5) cannot be determined from the results of these investigations. Since the slope of the straight lines (m) represents the direct effect of radiation on the transpiration rate, the decrease that occurs in it with increasing age of the plants must be associated with changes in the influence of radiation. If the latter is of a twofold nature, as already mentioned, these changes in m may be brought about in either of two ways. The changes that take place in the leaves as they grow older may be such that the coefficient of absorption for radiation is reduced so that the heating effect is less pronounced, or they may be such that the influence of radiation on the permeability of the protoplasm becomes less effective with increasing age.

Summary

1. The influence of radiation on the rate of transpiration of *Helianthus annuus* has been measured under natural conditions by the use of shade tents constructed so as to transmit different amounts of radiation and to permit such freedom of air circulation that other environmental factors were not altered appreciably.

2. The ten series made covered a rather wide range of conditions, but in all cases the relation between radiation intensity and transpiration rate was found to be linear within the limits of experimental error.

3. The results of all series could be satisfactorily represented by equations of the type $T = b + mR$, where T is the transpiration rate, R the radiation intensity, b the intercept on the T axis, and m the slope of the straight line.

4. It was found that b varied directly with the evaporating power of the air and m inversely with the age of the plants.

5. The fraction of the transpiration rate due to the direct effect of radiation is given by the ratio $mR/(mR + b)$, and for plants in full sunlight was found to vary from 38 to 81 per cent., depending largely upon the evaporating power of the air.

6. Calculations of probable errors indicate that on the average the results are accurate to within 5 per cent.

CARNEGIE INSTITUTION OF WASHINGTON
SANTA BARBARA, CALIFORNIA

LITERATURE CITED

1. ABBOT, C. G., FOWLE, F. E., and ALDRICH, L. B. Annals Astrophys. Obs. Smithsonian Inst. **4**: 65–79. 1922.
2. ARTHUR, J. M., and STEWART, W. D. Transpiration of tobacco plants in relation to radiant energy in the visible and infra-red. Contr. Boyce Thompson Inst. Plant Res. **5**: 483–501. 1933.
3. BIRGE, R. T. Probable values of the general physical constants. Phys. Rev. Suppl. **1**: 1–73. 1929.
4. BRIGGS, L. J., and SHANTZ, H. L. Daily transpiration during the normal growth period and its correlation with the weather. Jour. Agr. Res. **7**: 155–212. 1916.
5. ————, and ————. Hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agr. Res. **5**: 583–649. 1916.
6. CLEMENTS, F. E., and GOLDSMITH, G. W. The phytometer method in ecology. Carnegie Inst. Washington Publ. no. 356. 1924.
7. ————, and MARTIN, E. V. Effect of soil temperature on transpiration in *Helianthus annuus*. Plant Physiol. **9**: 619–630. 1934.
8. CLUM, H. H. The effect of transpiration and environmental factors on leaf temperature. Amer. Jour. Bot. **13**: 194–230. 1926.
9. IVANOV, L. A., and THIELMAN, M. Über den Einfluss des Lichtes verschiedener Wellenlänge auf die Transpiration der Pflanzen. Flora **116**: 296–311. 1923.
10. LLOYD, F. E. The physiology of stomata. Carnegie Inst. Washington Publ. no. 82. 1908.
11. LECLERC DU SABLON, M. Sur les causes du dégagement et de la rétention du vapeur d'eau chez les plantes. Rev. Gén. Bot. **25**: 49–83; 104–122. 1913.
12. LEPESCHKIN, W. W. Light and the permeability of protoplasm. Amer. Jour. Bot. **17**: 953–969. 1930.

Reprinted from PLANT PHYSIOLOGY, 9: 323–337, 1934.

APPLICATION OF CALORIMETRIC METHODS TO ECOLOGICAL RESEARCH

FRANCES L. LONG

The method of determining the heat of combustion by means of an oxygen bomb calorimeter has been adapted to plant studies of energy relations. This is based on standard chemical and physical practise, so that results obtained by one worker can be compared with those obtained by another. In general, it is the method by means of which heating values for coal and other fuels are obtained; the procedure that is used for determinations of caloric values for fats, proteins, and sugars upon which diets are based.

Prompt drying of plant material at moderate temperatures immediately after collecting is essential to accuracy, owing to the destructive effects of respiration and enzyme action. This demands an oven with considerable capacity, special ventilation, and uniformity of temperature throughout. An oven to meet these requirements was built for this work and is described in the paper by MARTIN.[1] The thermo-regulator is set for 75° C., since this temperature, aided by air currents, affords the most favorable condition for drying plant material of the type used here, with the minimum risk of destructive effects during the process. After drying, the material is ground fine, thoroughly mixed, and then made into pellets by means of a pellet press. To prevent these pellets from absorbing atmospheric moisture, which makes them so large and loose that they may fall from the capsule, they must be kept in a desiccator until required for use.

In calorimeters of the usual type having outside walls of bakelite or other insulating material, there is a heat interchange between the interior of the instrument and the surrounding air. Although the best insulation possible is used, it is still necessary to take heat losses into consideration and to make corrections for radiation to secure accurate results. The calorimeter used for the present studies was so constructed as to secure adiabatic conditions within the apparatus, thus avoiding heat leakage and the consequent necessity for corrections. The interior of the instrument, or calorimeter proper, is completely surrounded by jacketing walls through which water is circulated from a cold water tap and hot water boiler, so that the temperature can be regulated during the determination. By maintaining the jacket at a temperature corresponding with that of the calorimeter, all heat losses due to radiation are eliminated.

[1] MARTIN, E. V. Improved drying oven for plant material. Plant Physiol. 9: 1934.

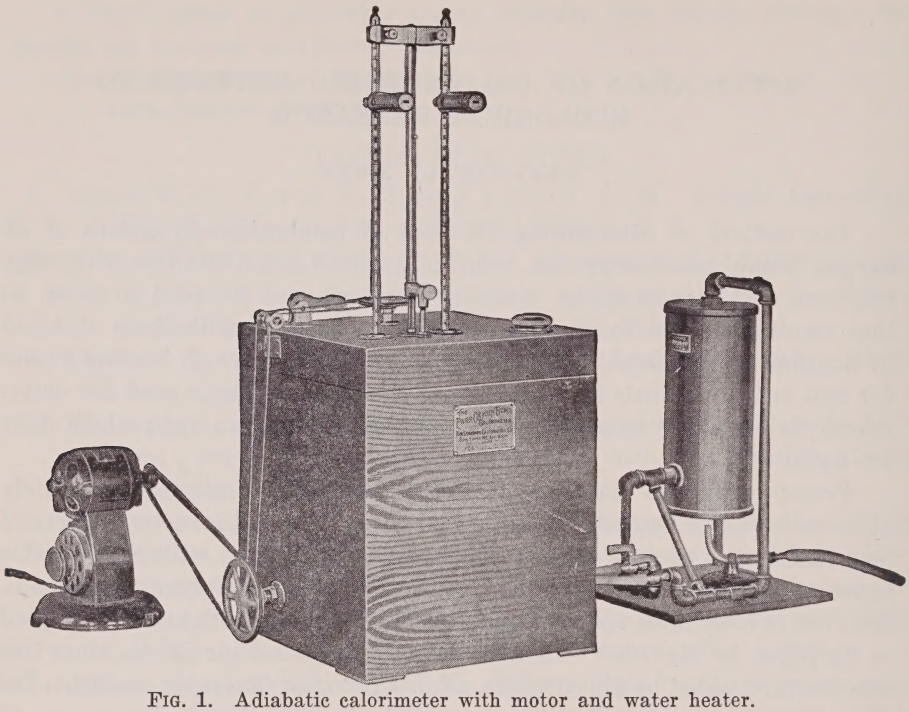

FIG. 1. Adiabatic calorimeter with motor and water heater.

Within the jacket is a metal casing, oval in form, which is so fitted as to allow a minimum air space between it and the oval bucket which is placed within it. The bucket is nickel-plated and highly polished to decrease thermal exchanges by radiation. It holds the 2 liters of water, the stirrer, and the thermometer.

For the determination, the pellets are weighed in a weighing bottle and then placed in a capsule which is suspended in the bomb. Both the bomb and the capsule are made of illium alloy, which resists the action of the nitric and sulphuric acids formed as a result of combustion. One of the necessary conditions is the avoidance of secondary reactions involving the oxidation or solution of the material of which the bomb is made.[2]

The fuse wire is adjusted so that it makes contact with the terminals and pellets. Then the illium bomb is filled with oxygen to 25 lb. pressure, placed in the calorimeter bucket and covered with 2 liters of distilled water. The lid to the calorimeter is pushed forward and closed, and the motor started in order to stir the water surrounding the bomb and jacket. When the switch is closed that makes the electrical connection, the fuse ignites

[2] For specific directions and details see Booklet 106, The oxygen bomb calorimeter. Standard Calorimeter Co., East Moline, Illinois.

the pellets in the capsule and is itself burned. From the rise of temperature of the water in the bucket and the grams dry weight of plant material in the pellets used, the number of calories of energy involved is calculated.

It is necessary to make corrections for the heat produced by the fuse wire, which for the kind of wire employed is 2.4 calories per cm. Because of the use of pure oxygen at high temperature and pressure, certain reactions take place that do not occur in the ordinary process of combustion. Thus the free nitrogen in the small amount of residual air present upon closing the instrument is partially oxidized to N_2O_5, which combines with the moisture present in the bomb to become HNO_3. Similarly the nitrogen of the plant material oxidizes to a greater or less extent to HNO_3. The sulphur in the pellets, which under ordinary conditions of combustion is oxidized to SO_2, is converted in the calorimeter to SO_3, and this to H_2SO_4.

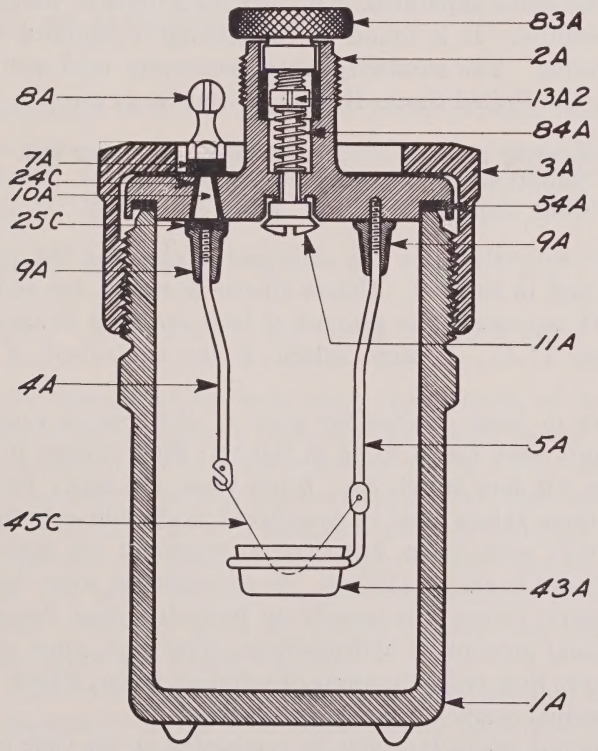

FIG. 2. Details of illium bomb: 1 A, illium cylinder; 2 A, illium cover, held in place by 3 A; 3 A, steel screw cap; 4 A, 5 A, electric terminals for fuse wire; 7 A, top terminal insulator; 8 A, top terminal; 9 A, illium locknut; 10 A, terminal cone; 11 A, illium valve; 13 A2, valve nut; 43 A, illium capsule for pellets; 54 A, cover gasket; 83 A, valve thumb nut; 84 A, valve spring; 24 C, cone insulator; 25 C, mica washer; 45 C, special fuse wire.

Since these acids represent a small portion of the energy produced, the bomb is rinsed out with distilled water, and the washings titrated with a standard solution of sodium carbonate made up of such a strength that each cc. represents one calorie. The calculations for a typical determination are shown in the example given here.

— Example —

$$\frac{\text{Water equivalent of calorimeter} \times \text{temp. rise °C.} - \text{corrections (wire + acid)}}{\text{Grams dry weight pellets}} = \text{calories per gram dry weight}$$

$$\frac{2450 \times 1.61 - 22.9}{1.1625} = 3365 \text{ calories per gram dry weight.}$$

The water equivalent of the calorimeter represents the amount of heat absorbed by the whole apparatus, including the 2 liters of water, per degree rise of temperature. It is found by combusting a standard substance of known heat value. The substances most commonly used with the values recognized by the United States Bureau of Standards are:

Benzoic acid	6320	calories per gm.
Naphthalene	9622	" " "
Cane sugar	3949	" " "

The water equivalent for the calorimeter used for the preceding example was found to be 2450. Unless otherwise stated, the small calorie is used here. It represents the amount of heat required to raise one cc. of water through 1° C. A large calorie is the equivalent of 1000 small calories.

The values in large calories for some of the organic compounds contained in plants were found to be as follows: Para rubber 10.2, resin 8.4, pure cellulose 4.0, and starch 3.8. Since there are many forms of resin, rubber, etc., these values must be considered as specific only for the plants from which they were taken, but they do represent the general range of values to be found in such materials. In consequence, when determinations show high caloric values it is usually an indication that the material contains an unusual amount of hydrocarbons, since each gram of these compounds has more than twice the value of cellulose, sugar, starch, and protein, the other principal components of plant tissues.

The number of grams that may be combusted at one time is determined not only by the size of the illium capsule, but also by the caloric value of the material. Three pellets weighing a total of 1 to 2 gm. make a convenient amount for each combustion. The thermometers used with this calorimeter read from 65° to 90° F., in 1/20 degree divisions. Two grams of *Helianthus annuus* seed when combusted in the calorimeter, give a rise of about

10° F., which would go beyond the limits of the thermometer if the initial temperature were above 80° F.; hence a safe rule is to limit the amount of material for each combustion to a maximum of 2 gm. and to have the initial temperature of the water within the thermometer range.

After combustion, the oxides of the mineral salts in the plant are found in the capsule as ash. In the giant cactus (*Carnegiea gigantea*), the ash of certain parts of the plant may be as high as 25.5 per cent. of the dry weight. Leaves of *Mesembryanthemum aequilaterale* contain about 25 per cent. of ash, while those of *Rosa, Rubus,* and *Prunus* yield approximately 6 per cent. ash on the same basis. In cases where the caloric value is not of special interest, but where it is desirable to know the amount of ash in various plant parts, the determinations may be made as indicated without recording the temperature rise. Ash analyses may also be made from the residue in the capsules when that is desirable. For example, table I gives WOLFF'S[3] analyses for the ash of *Helianthus annuus.*

TABLE I

COMPOSITION OF ASH OF *HELIANTHUS ANNUUS* IN PERCENTAGE

	K_2O	Na_2O	CaO	MgO	Fe_2O_3	P_2O_3	SO_2	SiO_2	Cl
	%	%	%	%	%	%	%	%	%
Seeds and fruits ...	16.23	7.41	7.63	12.29	1.6	35.43	2.34	14.65	2.42
Whole plant	60.77	1.84	12.56	6.75	0.22	8.89	1.71	0.88	6.38

Calorimetric determinations were made upon seeds of a number of species and life forms in order to ascertain the energy stored in each and to permit a comparison of the relative caloric values. The task of drying seeds before preparing the pellets is much simpler than with more succulent material, since respiration is at a minimum and the material is comparatively dry at the start. Combustion proceeds readily enough when whole seeds are used, but better average results were obtained from pellets of ground material. Table II gives the results obtained for the seeds of a number of crop plants and native conifers.

The great differences in growth during the early seedling stages, when the plant is dependent on the food stored in the seed, are more readily understood when one compares the energy supply upon which these plants may draw. For instance, *Pinus lambertiana* averaged 1222 calories per seed, 50 times as much as in *Pinus contorta murrayana.* The average for *Ricinus communis* was 2975 calories, or 2.4 times that of sugar pine and 20 times as much as for seeds of *Avena sativa.*

[3] WOLFF, EMIL. Aschen Analysen. 1871.

TABLE II

CALORIC AND ASH VALUES FOR VARIOUS SEEDS

SPECIES	CALORIES PER GM. DRY WEIGHT	CALORIES PER SEED	ASH
			%
Avena sativa	4238.3	143.4	2.5
Zea mays	4415.2	.....	.....
Sorghum vulgare	4017.6	144.6	1.2
Triticum sativum	4282.3	.....	0.8
Phaseolus coccineus	4282.2	.....	.....
Medicago sativa	5068.9	.....	.....
Cannabis sativa	5890.7	122.9	3.1
Brassica nigra	6049.5	.....	3.6
Helianthus annuus	6759.2	.....	.....
Ricinus communis	6834.7	2975.6	2.3
Pseudotsuga taxifolia	5998.3	59.9	1.5
Pinus ponderosa	5625.0	192.4	2.7
Pinus contorta murrayana	5989.2	26.7	2.7
Pinus lambertiana	6480.4	1221.8	1.7
Pinus flexilis	7117.7	372.9	2.6

The calorimetric method has been applied on an extensive scale to the plants obtained from the transplant and adaptation experiments carried on at the Alpine Laboratory and at Santa Barbara. Some representative results drawn from these are given in tables IV–IX. In addition, various series of determinations have been made for purposes of orientation, a typical example of which is furnished in table III, which records the caloric values for the largest individual of a widely spread group of cultivated sunflowers. At the time this plant was used, the achenes of the single large head were mature but not dry, while the lower leaves were slightly torn and beginning to turn brown. The leaves were cut in the order of position and labeled; they were weighed at once and the area taken by means of blue prints before drying. The stem, which was 2 meters tall, was cut into small pieces after weighing to insure rapid drying in the oven, and root and flower head were treated likewise. Each of these yielded much more material than needed for pellets, but an aliquot of each was utilized to secure a representative result (table III).

There proved to be less uniformity in the area, weight, and caloric value of adjacent leaves than was expected from their general appearance, a diversity probably due partly to shading and partly to competition between the leaves. Weights and calories rose more or less irregularly from a minimum at the bottom to a maximum in the upper third, to fall off rapidly to the top. By contrast, water gave the highest values in the lower third,

TABLE III

COMPARATIVE VALUES OF LEAVES AND ORGANS OF *HELIANTHUS ANNUUS*

LEAF	LEAF WEIGHT		WATER	ASH	LEAF AREA ONE SIDE	CALORIES PER GM. DRY WEIGHT	CALORIES IN WHOLE LEAF	RELATIVE VALUES
	WET	DRY						
	gm.	*gm.*	%	%	*sq. cm.*			
1 (top) ...	15.5	3.7	76.1	12.7	337	3993.2	14.780	43.8
2	19.6	4.3	78.0	12.4	339	3999.4	17.200	51.0
3	18.6	3.8	79.6	12.5	426	3971.0	15,100	44.8
4	38.8	8.2	78.9	11.4	770	3934.1	32,250	95.6
5	30.1	5.2	82.7	10.5	651	4051.6	21,100	62.5
6	36.1	7.5	79.3	11.8	709	4017.5	30,100	89.2
7	40.1	8.1	79.8	11.1	820	3907.9	31,600	93.6
8	24.7	4.5	81.8	13.7	526	3932.7	17,700	52.5
9	42.8	8.6	80.0	12.0	798	3922.7	33,750	100.0
10	29.9	5.5	81.6	12.5	629	4040.6	22,230	65.9
11	25.9	5.2	80.0	12.1	509	3935.2	20,740	60.6
12	33.7	6.6	80.5	12.7	648	3936.3	25,970	76.9
13	20.9	3.8	81.7	11.7	494	3896.3	14,800	43.8
14	29.3	5.7	80.6	12.8	583	3881.2	22,130	65.5
15	27.2	5.4	80.2	13.4	536	3821.4	20,650	61.2
16	17.4	2.9	83.3	13.4	420	3912.1	11,350	33.6
17	17.5	3.2	81.8	14.7	416	3866.9	12,390	36.7
18	17.1	3.0	82.5	14.8	403	3826.7	11,490	34.0
19	17.1	2.3	86.5	14.9	393	3742.4	8,610	25.6
20	16.2	2.6	84.0	15.7	392	3662.3	9,530	28.2
21	19.3	4.4	77.2	14.3	440	3769.6	16,600	49.2
22	12.8	2.4	81.2	16.6	296	3720.2	8,350	24.9
23	14.3	2.9	79.6	16.6	350	3557.7	13,310	39.4
24	11.9	2.3	80.6	16.4	283	3520.7	8,100	24.0
25	11.3	2.1	81.5	17.4	274	3546.7	7,450	22.1
26	8.2	1.4	82.9	17.9	220	3424.8	4,795	14.2
27	9.1	1.7	81.3	18.7	234	3497.6	5,950	17.6
Average	22.4	4.35	80.9	13.9	480	3825.5	16,954	.....
Whole plant	3638.8	578.8	82.8	8.8	.....	3983.5	2,320,964	100.0
Leaves	605.4	117.3	80.9	13.9	12,956	3825.5	457,725	19.7
Stem	1342.0	204.4	84.5	7.3	195 cm. high	3850.0	786,940	33.9
Root	419.4	87.5	79.2	8.8	.....	3951.0	345,713	14.8
Head	1272.0	169.6	86.6	5.2	30 cm. diam.	4307.7	730,586	31.6

TABLE IV

RELATION OF TOTAL CALORIES TO INTENSITY OF COMPETITION

SPECIES	DRY WEIGHT PER PLANT	WATER	ASH	CALORIES PER GM. DRY WT.	TOTAL CALORIES PER PLANT	RELATIVE VALUES
	gm.	%	%			
Helianthus annuus (young)						
4 normal	11.8	89.2	15.3	3807	44,923	100.0
16 "	9.5	86.0	15.0	3701	35,160	78.2
64 "	9.8	83.6	15.4	3664	35,907	79.9
128 "	7.2	90.5	16.7	3600	25,920	57.7
Helianthus annuus (mature)						
4 normal	352.5	83.2	8.9	3835	1,351,838	100.0
16 "	119.0	83.2	7.5	3934	468,146	34.6
16 suppressed	54.6	83.5	7.6	3897	212,776	15.7
64 normal	59.8	84.1	10.2	3813	228,017	16.8
64 suppressed	1.2	91.1	9.4	3819	4,583	0.3
128 normal	45.7	84.5	8.5	3799	173,614	12.8
128 suppressed	16.1	79.0	9.6	3717	59,844	4.4
Triticum sativum (young)						
4 normal	4.8	83.1	14.3	3585	17,208	100.0
16 "	3.4	83.3	25.1	3491	11,869	68.9
64 "	2.3	81.6	25.5	3463	7,965	46.2
Triticum sativum (mature)						
4 normal	65.5	66.0	4.2	4042	264,751	100.0
16 "	50.5	63.0	3.5	4103	207,202	78.2
64 "	11.6	58.0	8.6	3828	44,405	16.7
128 "	8.4	54.0	14.5	3594	30,190	11.4
Zea mays (young)						
4 normal	42.3	80.0	10.8	4006	169,454	100.0
16 "	20.7	86.3	12.3	3868	80,068	47.2
64 "	24.3	84.3	10.9	3955	86,107	50.8
128 "	18.1	86.4	8.2	3747	67,821	40.0
Zea mays (mature)						
4 normal	241.7	84.9	3.5	4053	979,610	100.0
16 "	99.5	75.2	5.1	3961	394,120	40.0
16 suppressed	27.2	72.7	4.1	3899	106,053	10.8
64 normal	44.3	78.1	4.6	3909	173,169	17.6
64 suppressed	10.6	80.7	10.1	3828	40,577	4.1
Campanula medium						
4 normal	310.7	76.0	10.4	4498	1,397,529	100.0
64 "	37.0	78.0	10.6	3834	141,969	10.1
Plantago lanceolata						
4 normal	283.7	74.0	15.0	3628	1,029,264	100.0
64 suppressed	5.2	70.0	19.4	3507	18,236	1.7

and ash at the bottom, the latter decreasing rather regularly and the former rather irregularly to the top. The caloric value per gram was highest in the head, owing to the storage of oil in the seeds.

For the study of adaptation under different degrees of competition, a number of cultures have been established each year, with frequent changes of the species employed. Each culture contained four units 4 ft. square, separated by paths 1.5 ft. wide, in which the respective densities were 4, 16, 64, and 128 plants. The bed with four individuals served as a standard for the other three, in each of which the density was sufficient to produce a smaller or larger number of suppressed plants (table IV).

As would be expected, the young plants showed less response to crowding, since the demands of each individual had not reached the maximum. The mature plants yielded consistent and striking results throughout, the three crop species giving nearly identical relative values in the two higher densities. The suppressed plants were naturally more variable, but for the most part averaged about a fourth of the value for the normal or dominant individuals.

In all competition cultures without a buffer margin, the outermost plants profit from the lack of competition on the edge, the individuals at each corner often being especially well grown. Conditions as to water content and nutrients are much the same on all four sides, but the light intensity is distinctly higher on the south (table V).

The plants on the south margin were approximately 2.5 times higher in calories than were those on the north, primarily as a consequence of

TABLE V

TOTAL CALORIES PRODUCED UNDER COMPETITION AT SAME DENSITY

HELIANTHUS ANNUUS	WEIGHT OF PLANT		WATER	ASH	CALORIES PER GM. DRY WT.	CALORIES PER PLANT	RELATIVE VALUES
	WET	DRY					
	gm.	*gm.*	%	%			
South margin	938.2	152.8	83.7	7.1	4071	622,049	100.0
North margin	416.1	61.5	84.9	8.1	3925	242,003	38.9
North suppressed	261.4	34.0	87.0	7.8	4018	136,612	21.9
Center dominant	121.1	21.3	82.4	7.8	3855	82,112	13.0
Center suppressed	83.1	9.8	85.8	8.0	3751	36,560	5.8

better illumination, while dominant plants on the north were about twice as large as the suppressed ones. The caloric values in the center were distinctly less for all individuals, while the suppressed were less than half as large as the dominants and contained but 5 per cent. as many calories as the plants on the south margin.

In seeking the functional explanation of the striking modifications and transformations secured under low light intensities, the calorimeter has proved an effective adjunct to measurements of transpiration and photosynthate. The species listed in table VI were grown in lath houses with light values of 12 to 4 per cent. of sunlight, the controls being located in sunshine.

The various species differ strikingly in their efficiency under the reduced intensities. The highest values in light of 12 per cent. were for *Solanum, Verbesina,* and *Mentzelia,* with relative performances of 15, 14, and 13 approximately, while the lowest were for *Allium, Madia,* and *Helianthus,* all at about 1 per cent. The best relative production in 4 per cent. light was that of *Clarkia* at 7.4, followed closely by *Solanum* at 6.4; the poorest performance again was that of *Allium, Madia,* and *Helianthus,* with half or less of 1 per cent. The average production in the deeper shade was 2.7, in the lighter shade 6.3, these values being in fair agreement with the respective light intensities. The number of calories may also vary greatly from year to year in correspondence with climatic conditions, especially sunshine and temperature, as is evidenced by the results obtained with *Helianthus* and *Plantago* in successive years.

In the endeavor to ascertain the effects of different lengths of day on species growing in the experimental garden, dark tents were employed to reduce the time of exposure to daylight from 13 hours in the long-day series to 9 in the mid-day and 5 in the short-day series. The plants were regularly best-grown in the longer exposure, and flowering occurred about two weeks earlier, leaves and flowers both being deeper colored. The mid-day series was intermediate in all respects, except that the stems were tallest. In the short-day tents the plants were shortest and palest, the flowers fewer, smaller and paler, blooming later than in either of the other series. In all cases the results were similar to those obtained in the lath houses, and this fact is reflected in the values shown in table VII, although the exposure to direct sunlight gave higher amounts in practically all cases.

The relative values differ much for the different species, the highest being given by *Verbesina* and the lowest by *Zinnia,* thus reflecting their abilities to grow and become modified in the shade. In general terms, the average production in the mid-day series with two-thirds as much sunshine was a little more than one-third of that in the long-day; and in the short-day with four hours less, it was again slightly more than one-third.

TABLE VI

RELATION OF TOTAL CALORIES TO LIGHT INTENSITY

SPECIES	LIGHT VALUES	WEIGHT OF PLANT		WATER	ASH	CALORIES PER GM. DRY WT.	CALORIES PER PLANT	RELATIVE VALUES
		WET	DRY					
	%	*gm.*	*gm.*	%	%			
Allium cepa	Sun	348.0	35.0	90.0	11.1	3777	132,195	100.0
	12	3.1	0.22	93.0	16.9	3762	817	1.0
	4	1.7	0.13	92.0	20.6	3552	462	0.6
Clarkia elegans	Sun	225.0	45.0	80.0	5.8	3980	179,100	100.0
	12	16.5	3.8	74.0	9.7	3821	14,520	8.7
	4	19.0	3.6	79.0	8.1	3757	13,525	7.4
Gilia capitata	Sun	317.5	81.5	74.0	6.0	4204	342,626	100.0
	12	12.1	2.3	81.0	7.4	4074	9,370	2.7
	4	4.2	0.9	79.0	14.1	3835	3,452	1.0
Helianthus annuus (1930)	Sun	950.6	217.7	77.1	5.7	3996	869,929	100.0
	12	25.0	2.1	91.6	10.4	3645	7,655	0.8
	4	5.5	0.16	97.1	10.4	3625	580	0.06
Helianthus annuus (1931)	Sun	602.0	149.2	75.0	4.5	3955	590,086	100.0
	12	52.3	6.1	88.0	12.8	3593	22,527	3.8
	4	8.7	1.2	86.0	16.6	3348	4,018	0.6
Madia elegans	Sun	1,260.0	394.1	69.0	8.5	4175	1,645,368	100.0
	12	24.9	5.3	79.0	18.6	3464	18,359	1.1
	4	11.0	2.3	79.0	20.5	3286	7,558	0.4
Mentzelia lindleyi	Sun	179.1	24.0	86.8	14.6	3581	88,344	100.0
	12	35.3	3.5	90.1	21.0	3323	11,631	13.1
	4	7.6	1.0	86.9	26.4	3110	3,110	3.5
Plantago lanceolata (1930)	Sun	149.3	22.4	85.0	14.3	3641	81,558	100.0
	12	11.1	1.4	87.4	13.7	3502	4,903	6.1
	4	10.7	0.9	92.0	19.0	3368	3,031	3.5
Plantago lanceolata (1931)	Sun	520.0	133.0	74.0	11.3	3826	508,858	100.0
	12	46.1	4.1	91.0	21.5	3202	13,128	2.5
	4	34.9	3.1	91.0	21.5	3127	9,694	1.8
Rumex patientia	Sun	279.3	58.8	79.0	11.3	3834	225,439	100.0
	12	16.1	3.9	76.0	18.3	3707	14,457	6.4
	4	7.2	1.0	86.0	19.4	3681	3,681	1.6
Solanum tuberosum	Sun	200.7	50.1	75.0	13.3	3819	191,332	100.0
	12	84.3	8.8	90.0	20.1	3417	30,070	15.6
	4	42.2	4.1	91.0	24.1	3169	12,993	6.7
Verbesina encelioides	Sun	540.0	125.7	77.0	10.3	3788	476,152	100.0
	12	95.7	19.3	80.0	15.3	3433	66,257	13.9
	4	48.8	6.7	86.0	21.2	3082	20,649	4.0

TABLE VII

RELATION OF TOTAL CALORIES TO LENGTH OF DAY

SPECIES	LIGHT	WEIGHT OF PLANT		WATER	ASH	CALORIES PER GM. DRY WT.	CALORIES PER PLANT	RELATIVE VALUES
		WET	DRY					
		gm.	*gm.*	%	%			
Gilia capitata	Long-day	317.5	81.5	74.0	6.0	4204	342,626	100.0
	Mid-day	181.5	36.7	80.0	11.1	3705	135,974	39.7
	Short-day	55.5	11.0	80.0	19.0	3482	38,302	11.1
Phacelia grandiflora	Long-day	223.0	58.0	74.0	18.5	3446	199,868	100.0
	Mid-day	60.5	13.3	78.0	20.4	3311	44,042	22.0
	Short-day	38.0	8.5	78.0	26.4	3094	26,297	13.1
Rumex patientia	Long-day	279.3	58.8	79.0	11.3	3834	225,439	100.0
	Mid-day	102.0	27.5	73.0	12.4	3774	103,785	46.0
	Short-day	21.8	3.8	83.0	15.6	3688	14,014	6.2
Verbesina encelioides	Long-day	117.4	25.3	78.5	11.5	3701	93,653	100.0
	Mid-day	142.1	20.7	85.4	11.5	3563	74,100	79.1
	Short-day	71.7	9.3	87.1	13.8	3488	32,439	34.6
Zinnia grandiflora	Long-day	88.0	18.8	79.0	11.3	3809	71,600	100.0
	Mid-day	9.8	2.4	75.0	13.9	3567	8,561	11.9
	Short-day	8.8	1.6	82.0	21.0	3247	3,247	4.5

TABLE VIII

RELATION OF TOTAL CALORIES TO AMOUNT OF NUTRIENTS

SPECIES	NUTRIENT RATIO	WEIGHT OF PLANT		WATER	ASH	CALORIES PER GM. DRY WT.	CALORIES PER PLANT	RELATIVE VALUES
		WET	DRY					
		gm.	*gm.*	%	%			
Calendula officinalis	2N: 2W	694.5	120.0	83.0	11.9	3871	464,520	100.0
	1N: 1W	166.5	37.5	78.0	16.2	3742	140,325	30.2
	0N: 0W	100.5	18.2	82.0	17.0	3608	65,666	14.1
Gilia capitata	2N: 2W	635.1	185.5	71.0	5.8	4268	791,714	100.0
	1N: 1W	102.5	28.7	72.0	5.1	4282	122,893	15.5
	0N: 0W	68.1	18.2	73.0	5.7	4205	76,531	9.5
Madia elegans	2N: 2W	253.5	103.0	59.0	14.7	3950	406,850	100.0
	1N: 1W	110.0	45.5	59.0	13.6	3801	172,946	42.5
	0N: 0W	68.5	21.6	68.0	18.9	3519	76,010	18.6
Petunia hybrida	2N: 2W	56.7	10.5	82.0	14.4	3747	39,344	100.0
	1N: 1W	55.5	9.8	82.0	18.8	3548	34,770	90.7
	0N: 0W	8.8	1.7	80.0	24.8	3564	6,059	15.8
Solanum tuberosum	2N: 2W	235.0	58.5	75.0	9.5	3932	230,022	100.0
	1N: 1W	121.0	26.9	78.0	12.5	3805	102,355	44.4
	0N: 0W	42.0	8.8	79.0	16.2	3783	33,290	14.4

In the series designed to test the response to increased nutrients, commercial fertilizer was applied to one row of beds in the amount regularly used by gardeners for the soil concerned, and in twice the amount. The supply of water was similarly increased to maintain the soil solution at about normal density, while in the control row no addition was made to the amount received from rainfall, and no nutrient was added (table VIII).

As was to be expected, the addition of nutrients and water greatly increased the size of the plants in comparison with the controls, the number of shoots being greater and the leaves larger and more deeply colored. The difference between the several species was marked, the maximum effect being found in *Gilia* with 11 times the control and the minimum in *Madia* with 5.5 times.

The soil series consisted of soil pits in three rows, one containing fertile garden loam, another a fertile black clay called adobe, and a third, sand. While soil is the remote factor, the immediate response is to water content, the fluctuations of which are automatically regulated by soil texture under the condition of equal watering (table IX).

TABLE IX

RELATION OF TOTAL CALORIES TO TYPE OF SOIL

SPECIES	SOIL	WEIGHT OF PLANT		WATER	ASH	CALORIES PER GM. DRY WT.	CALORIES PER PLANT
		WET	DRY				
		gm.	*gm.*	%	%		
Madia elegans	Loam	1,260.0	394.1	69.0	8.5	4175.0	1,645,368
	Adobe	422.0	182.5	57.0	8.1	4105.0	749,163
	Sand	275.5	111.8	60.0	14.9	3973.0	433,000
Plantago lanceolata	Loam	480.0	106.4	78.0	8.3	4008.2	426,472
	Adobe	334.5	70.7	79.0	13.5	3709.4	263,254
	Sand	65.0	9.6	85.0	13.6	3319.8	31,870
Solanum tuberosum	Loam	200.0	50.1	75.0	13.3	3819.4	191,352
	Adobe	30.0	7.5	75.0	6.8	3809.5	28,580
	Sand	15.8	1.3	80.0	7.4	3795.6	4,930

In all three species selected, the growth in loam was two to several times that in the adobe, and growth in the latter two to eight times that in the sand. In general the soil series yielded the most consistent and striking modifications in response to varying water content.

From the preceding data it is evident that the calorimetric method introduces into ecology and the related sciences, agriculture, horticulture, forestry, etc., an accurate chemical procedure for measuring performance. It makes it possible to ascertain in exact terms not only how much energy is utilized, but also how much is stored in seed, bud, or underground part

against the time of future need. The efficiency of the individual plant, variety, or species may be compared with that of others grown under the same conditions, and thus serve as a definite basis for selection or breeding. The plant itself may be employed as an index of the energy available at different altitudes or latitude, under various natural canopies or artificial covers, or in connection with long-day and short-day exposures, as in the work of GARNER and ALLARD. It also becomes possible to obtain the plant's reaction to the influence of varying amounts of water, in the case of irrigated crops for example, of soil nutrients and fertilizers, of the air content in the case of water-logged soils, and so forth. The effect of the time and intensity of grazing range grasses or time of cutting fields of alfalfa can be measured with signal accuracy, and perhaps even a forecast made of the next season's growth on the basis of the amount of stored food.

Furthermore, two processes of fundamental importance in plant life, competition in the community and adaptation in the individual, can be evaluated more accurately and objectively by means of the calorimeter. The degree of competition between plants determines not only the amount of energy available for each, but also the conditions under which it can be utilized, while the energy actually transformed represents the performance of the several competitors.

CARNEGIE INSTITUTION OF WASHINGTON
SANTA BARBARA, CALIFORNIA

Reprinted from PLANT PHYSIOLOGY, 9: 689–692, 1934.

A LARGE-CAPACITY DRYING OVEN WITH CONSTANT UNIFORM TEMPERATURE AND FORCED VENTILATION

EMMETT V. MARTIN

Temperature and rate of drying are important factors in desiccation of plant material for analysis. Various temperatures, ranging from 30° to 105° C., have been used for this purpose, although there is no particular one which is entirely satisfactory in all respects. In the higher range there may be a decrease of soluble nitrogen by coagulation, and caramelization of the sugars may occur, while at the lower values there will be enzyme action and respiration. TOTTINGHAM and LINK[1] have made a special study of methods of desiccation of plant tissue, and have given data showing that preparation under widely different conditions yields results that are not comparable. They conclude that material which dries readily undergoes least destructive change with a temperature of about 65° C. When the material is dried in an oven with very little ventilation, the humidity soon becomes so high that drying proceeds very slowly, thus allowing destructive action to continue for a longer period of time. If one wishes to compare analyses of stems and leaves, the former should be sliced longitudinally into slender strips so that they will dry more quickly. Leaves also can be cut into a number of pieces to similar advantage. When the material is placed in the oven, it should be well spread out to allow good circulation of air around all parts.

In the preparation of plant tissue for analysis, therefore, it is desirable to use an oven that has a fairly constant uniform temperature and good ventilation. Furthermore, if considerable quantities are to be dried, a rather large capacity is needed. Such ovens are obtainable, but the expense may in some cases be prohibitive. It is the purpose of this paper to describe an oven that can be constructed by local sheet-metal workmen at much lower cost than its equivalent can be purchased from manufacturing companies.

In figure 1 is shown a diagram of a cross-section through the center of the oven, drawn to scale. It is made up of three separate sections, *A*, *B*, and *C*. Section *A* comprises the oven proper, *C* contains the heaters, and *B* provides extra insulation between *A* and *C*. The outside dimensions of

[1] LINK, K. P., and TOTTINGHAM, W. E. Effects of the method of desiccation on the carbohydrates of plant tissue. Jour. Amer. Chem. Soc. 45: 439–447. 1923 (also 47: 470–476. 1925).

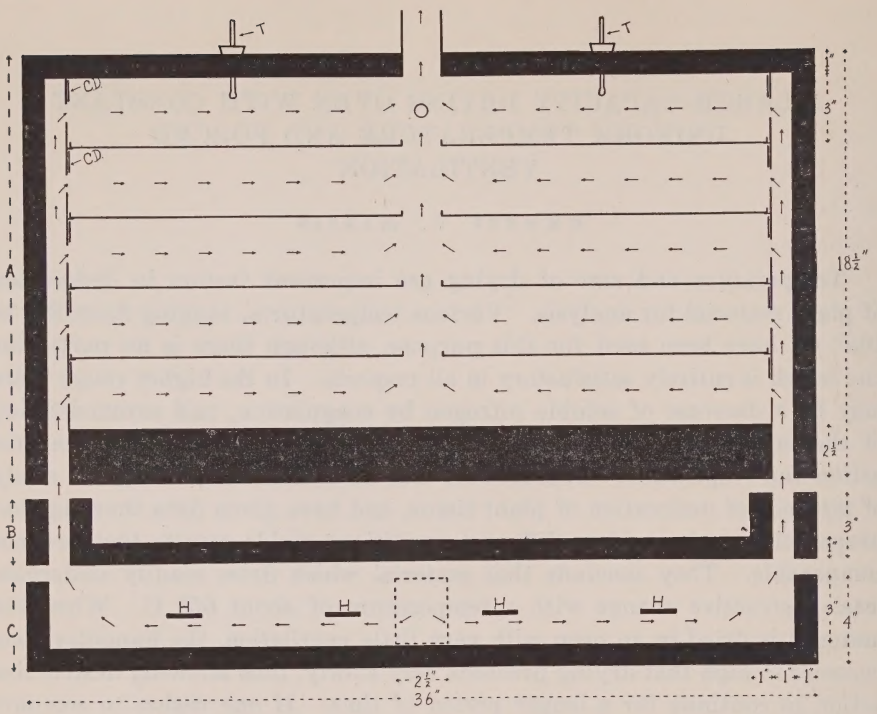

FIG. 1. Diagram of cross-section through center of oven, drawn to scale.

section *A* are $36'' \times 20'' \times 18\frac{1}{2}''$, the inside are $32'' \times 18'' \times 15''$, while others are shown in the illustration.

The walls are constructed of no. 26 galvanized sheet-iron of two layers 1″ apart, except on the floor of section *A* where the spacing is $2\frac{1}{2}''$. The spaces between layers are filled at the rate of 12 pounds per cubic foot with loose rock wool, manufactured by the Gimco Rock Wool Products Co. The four shelves in section *A* are made of no. 24 galvanized sheet-iron, with the edges bent over $\frac{1}{4}''$ for added strength. In the center of each shelf and in the top of the oven there is a slot $1\frac{1}{2}'' \times 16''$ to allow for the passage of air. The shelves rest on slides at each end of the oven and are removable.

The amount of air that passes over each shelf is controlled by a diaphragm opening at each end (fig. 1). These openings are $\frac{3}{4}'' \times 16''$ and can be partially or completely closed by means of covers (*C, D*). These covers are adjustable and are held in place by means of a thumbscrew in a slot at each end.

Heat is furnished by four coils (*H*) of no. 26 B. & S. gauge chromel A wire wound on strips of transite $\frac{1}{4}'' \times 1\frac{1}{2}'' \times 18''$, supported in place by angle irons. The two outer coils are connected in series and draw 405 watts from a 110-volt A.C. source, while the two inner ones, also in series, take 235

watts. When the oven is in operation the 405-watt coils are heating continuously, but the 235-watt coils are controlled by a DeKhotinsky bimetallic thermoregulator which projects through the rear wall into the center of the space above the top shelf (shown as small circle in figure 1). Electrical connections to the heaters are made through binding posts insulated from the walls by fiber tubing and washers.

Ventilation is produced by a no. 1 baby conoidal blower manufactured by the Buffalo Forge Co. This blower is mounted on a small platform attached to the rear of section *C*. Air is passed from the blower to this section through a short metal tube, which is round at the blower end and square at the oven end. In this tube is mounted an adjustable damper for the control of air flow. The blower has a capacity of 78 cubic feet of air per minute, but its delivery is limited in this case to approximately 12 cubic feet per minute. With this rate of flow the air in the oven is replaced more than twice per minute.

The course of air through the oven is indicated in the figure by small arrows. Leakage between the sections is prevented by padding the points of contact with asbestos, and the sections are prevented from slipping on each other by flanges. The diaphragm covers (*C*, *D*) are adjusted so that approximately the same amount of air passes over each shelf. To accomplish this, the top covers are nearly closed and the bottom ones wide open; the openings of the others are graduated accordingly.

Between sections *A* and *B* is an air space open at the front and back to the outside. This space and the thick floor of *A* effectively prevent any transfer of heat from the heaters through the floors to the lower shelf. This is necessary in order to obtain uniform temperature in the oven.

Measurements of the temperature distribution within the oven were made by means of six thermocouples operating simultaneously at different points. Readings were taken every few minutes over a complete cycle of opening and closing of the thermostat contacts. The couples were then moved to other points and further readings taken. This process was repeated until all regions of the oven had been covered. The maximum difference in temperature found was 7° C., and its variation at any particular point was not more than 2° C. from the mean at that point. During these tests the thermostat was set at approximately 65° C., registered by thermometers marked *T* in figure 1.

Summary

1. For preparation of plant tissues for analysis, it is desirable to have a drying oven of fairly constant uniform temperature, good ventilation and large capacity.

2. The oven described has the following advantages and characteristics:

a) It can be made by local sheet-metal workmen at much lower cost than its equivalent can be purchased from manufacturing companies.

b) It has a volume of 5 cubic feet and a shelf space of 20 square feet.

c) No two points differ in temperature by more than 7° C.

d) The temperature at any particular point does not vary more than 2° C. from the mean at that point.

e) The air is replaced more than twice per minute.

f) Its maximum power requirement is 640 watts.

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